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ENTOMOLOGIST'S GAZETTE

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All communications to the Editor, 22, Harlington Road East, Feltham, Middlesex, England. Telephone Feltham 3740

ENTOMOLOGIST'S GAZETTE is published Quarterly in January, April, July and October. The Subscription Rate is one pound per year. For Advertising rates apply to The Editor.

NEWS AND VIEWS

It has not proved possible to complete the index to Volume 5 for distribution with this number; it will either be sent out with the April number or sent to subscribers under separate cover.

Mr. R. M. Mere undertook the heavy work of preparing the index to volume 5, and we are very grateful to him. Mr. R. D. Weal has now kindly consented to become our indexer, and we welcome his help.

Many readers have asked whether it is still possible to have their *Gazettes* bound through us. We do undertake binding in standard covers (dark blue cloth) at the price of 9s. 6d. per volume, post free. Copies for binding should be sent to the Editor.

SUBSCRIBERS' NOTICES. We have decided to devote the inside back cover of the *Gazette* to *Subscribers' Notices*. This service will, of course, be free to all subscribers, and items for insertion should be sent to the Assistant Editor, Mr. A. E. Gardner, F.R.E.S., 29 Glenfield Road, Banstead, Surrey.

DERMAPTERA & ORTHOPTERA IN S.W. SUSSEX

By A. E. Gardner, F.R.E.S.

The following species were observed between 15th and 28th August, 1954.

DERMAPTERA

Forficula auricularia L. Common in debris and old nettle beds at Selsey, Bracklesham and Birdham.

F. Lesnei Finot. Common in old nettle beds bordering the Chichester Canal between Birdham and Hunston. Found sparingly at Manhood End in nettles, a few also obtained by beating elm and oak.

ORTHOPTERA

Meconema thalassinum (De Geer). Fairly common at Birdham and Manhood End. A few specimens were obtained by beating oaks, but were more abundant on elm. Prior to 25th August, only penultimate instar larvae were found. After this date mature specimens were taken. A number of immature larvae were kept in captivity and ecdysis was observed to take place only early in the morning or late at night. A captive male was heard 'drumming' on three separate occasions. The sound was of short duration, less than a second, and was repeated after a brief interval. From the loud noise produced it sounded as if the tip of the abdomen was rapidly vibrated against the celluloid wall of the breeding cage. This could not be verified, as when brought into the light drumming ceased. This observation is in variance to that of Currie (1953).

Tettigonia viridissima L. Several specimens seen on thistles at Bracklesham. Fairly common at Pagham.

Conocephalus dorsalis (Latr.). Extremely common along the Broad Rife at Bracklesham, where they were found on *Carex* sp. and Sea Lavender *Limonium vulgare*. In dull weather they were difficult to find, but after a short spell of sunshine became very active.

Chorthippus brunneus (Thunb.). Fairly common in dry areas at Bracklesham and Birdham.

C. albomarginatus (De Geer). Abundant between Bracklesham and Selsey. The specimens found along the banks of the Broad Rife were noticeably more green in colour as compared with examples examined from the dry grass areas bordering the beach.

C. parallelus (Zett.). Fairly common in meadows at Bracklesham, Selsey and Birdham.

Acknowledgment

I am indebted to Dr. D. K. McE. Kevan for drawing my attention to the interesting paper on *Meconema thalassinum*, by Mr. Currie.

LITERATURE CONSULTED

Burr, M., 1936. *British Grasshoppers and their Allies, a Stimulus to their Study*. London.

Currie, P. W. E., 1953. The 'Drumming' of *Meconema thalassinum* Fabr. *Ent. Rec.*, **65**: 93-94.

ABERRATIONS OF BRITISH LEPIDOPTERA

By E. A. COCKAYNE, O.B.E., D.M., F.R.C.P.

The following aberrations are in the Rothschild-Cockayne-Kettlewell collection in the British Museum, with the exception of those named by Bytinski-Salz.

AEGERIDAE

Aegeria culiciformis Linnaeus ab. **albocingulata** ab. nov.

The abdominal belt is white instead of red; the patch on the inner aspect of the tibia and the whole of the tarsus is also white instead of yellowish.

Type: ♂: Folkestone, Kent, 1875, W. Purdey. (B. Whitehouse Coll.), Cockayne Coll.

Allotype: ♀: Wyre Forest, Worcs., 6, vi. 1897, P. W. Abbott. (B. Whitehouse Coll.) Cockayne Coll.

Paratypes: 2♂: 1♂; loc. incog., 14, vi. 1887, W. W. Wood.
1♂: Colchester, Essex, bred 1895 by Harwood. (Gilles Coll.) Cockayne Coll.

HEPIALIDAE

Bytinski-Salz (*Ent. Record* 1939. **51**: 81-84) reviews the nomenclature of *Hepialus humuli* L., and deals with specimens from Shetland, pp. 82-83. He gives Edward Newman's original description (*Entomologist*, 1865. **2**: 162). 'Abnormal series of *Hepialus humuli* taken in the Shetland Isles. I have been led to doubt the accuracy of the conclusion at which Entomologists have arrived, that all specimens of *Hepialus humuli* with white wings are males, and all those with fulvous wings females. In some specimens the forewings are tinted with yellow, while the hindwings are pure white; in others the forewings are pure white, the hindwings dark fuscous. In those specimens supposed from their general appearance to be females, the tint is paler than in the Southern specimens and more approaches dull lemon-yellow than fulvous; the body is uniformly dark fuscous and the hindwings, when tinted at all, are of the same dark colour. I would propose for them the name *Hepialus thulensis* as a species.'

In the next year Crotch says it is not a species but a subspecies (using var. in Staudinger's sense) of *Hepialus humuli*. Bytinski-Salz then says it is clear that as the type form of var. *thulensis*, Newman male specimens with dull lemon-yellow colour must be chosen, but as the original description of Newman does not mention whether dark markings on the forewing are present or not, it was impossible to determine the right form to which Newman applied his name, until H. J. Turner had traced Newman's original series in the British Museum. Turner said there was a male labelled '*thulensis* Crotch' with yellowish forewings and heavy brown markings, like the one

figured Pl. 7., fig. 3, and Bytinski-Salz chose this as the Type of ssp. *thulensis* Newman. He then says that Staudinger's var. *hethlandica* 1871 (*Cat.* ed 2, p. 60) is a synonym. He proceeds—ssp. *thulensis* varies considerably in respect to coloration and designs of the forewing. The principal forms of males may be distinguished by the following Key:

1. Forewing yellow, heavily marked with dark designs; ssp. *thulensis* f. *thulensis* Newm. (syn. *hethlandica* Stdgr.).
2. Forewing yellow, without dark designs; ssp. *thulensis* f. *uniformis*.
3. Forewing white, heavily marked with dark designs; ssp. *thulensis* f. *albida*.

[4. Forewing white, without dark designs; ssp. *humuli* L.]

Uniformis f. nov. (fig. 4). Ground colour of the forewing ochreous-yellow, as in f. *thulensis* Newm., but entirely without dark designs.

E. *albida* f. nov. (fig. 2). Ground colour of the forewing silky white as in *humuli* L., with distinct brown markings as in *thulensis*. The hindwings vary much from white to dark grey, with radial white suffusion from the base.

Mr. G. H. E. Hopkins has helped me with this muddled paper. It is clear that *thulensis* Newm. is a subspecific name, and the selection by Bytinski-Salz of the form with yellowish forewings and heavy brown markings in the male as the lectotype is valid. Staudinger, 1871, in Staudinger and Wocke, *Cat. des Lep.*, ed. 2, p. 60, gives a.v. *hethlandica* (♂ al. ant. flaviolis, fulvo striatis), i.e., art oder var., species or subspecies.

Hethlandica is therefore a synonym of *thulensis* Newm.; f. *thulensis* means ab. *thulensis*, but this is an unnecessary name since it is the typical form.

The forms recognised by Bytinski-Salz are:—

(1) The typical form of the ssp., forewing yellow, with heavy dark markings.

(2) f. = ab. *uniformis* B-S., forewing yellowish without markings.

(3) f. = ab. *albida* B-S., forewing white with heavy dark markings.

The form with white forewings, called ssp. *humuli*, placed in square brackets may be intended for Shetland males, but these are small and have dark thorax and abdomen. In that case it is a misapplication of ssp. *humuli* as defined by Linnaeus and has no validity. On the other hand Bytinski-Salz may have been so unobservant that he did not notice this difference and thought that ssp. *thulensis* occurred in one part of Shetland and the Linnaean ssp. *humuli* in another.

If he had not written this misguided paper I should have said that the plain white male was the typical *thulensis* and regarded the other three as aberrations.

In the so-called plain yellow male photography shows that the pattern is present, although not visible to the human eye.

The plain white male does not appear to have been named.

In addition to those named by Bytinski-Salz I am describing and naming the following aberrations.

Hepialus humuli Linnaeus ssp. *thulensis* Newman ab. **fumosa** ab. nov.

Plate 1. figs. 1, 3, 4.

The forewing is suffused with dark smoky brownish grey; the hindwing is blackish grey. The smoky suffusion may occur in the white form with more or less normal markings, which are blackish-brown instead of rufous, or in the yellowish form. It may also occur in the white or yellowish form with the markings nearly obsolete, ab. *unifcrmis* B-T. The female is smoky brown.

Type ♂: Shetland, 1908, McArthur. (Bright Coll.) Rothschild Coll.

Allotype ♀: Shetland, 1907, P. M. Bright (Bright Coll.) Rothschild Coll.

Paratypes 4♂, 1♀: 1♂; Shetland, W. Salvage, 1908, (Bright Coll.) Rothschild Coll.: 1♂; Shetland, 1907, P. M. Bright (Bright Coll.) Rothschild Coll.: 1♂; Unst, 1 892 (McArthur Coll.), yellowish unicolorous form: 1♂; Shetland, 1908, W. Salvage (Bright Coll.) Rothschild Coll.: 1♀; Shetland, P. M. Bright (Bright Coll.) Rothschild Coll.

Hepialus humuli Linnaeus ab. **radiata** ab. nov.

Plate 1. figs. 2, 5.

From the oblique line on the forewing rays of the same colour run out along the nervures to the termen. The aberration appears to be much commoner in ssp. *thulensis* Newman, and of course in the male sex is confined to this subspecies.

Type ♂: Unst, Shetland, 1895, Wm. Reid. R. Adkin Coll.

Allotype ♀: Shetland, 1902, (McArthur Coll.) R. Adkin Coll.

Paratypes 1♂, 2♀: 1♂; Shetland 1895, Rothschild Coll.: 1♀; Shetland, 1906, (Bright Coll.) Rothschild Coll.: 1♀; Shetland, 1907, P. M. Bright, Bankes Coll.

In 1953 Mr. David Cunningham caught a small male with dark thorax and abdomen, white forewings with dark brown pattern and dark hindwings. The forewings were radiated. He caught it himself near Dumfries. He has kindly presented it to the Rothschild-Cockayne-Kettlewell collection. It is indistinguishable from some Shetland specimens. A friend of his caught another somewhat similar one near Dumfries. I can offer no explanation for their occurrence, or rather I do not intend to offer one.

Hepialus lupulina Linnaeus ab. **albomarginata** ab. nov.

The usual white spots along the termen are fused to form a narrow white marginal stripe.

Type ♀: Feering, Essex, 11. vi. 1910, F. C. Reid, Rothschild Coll.

Hepialus lupulina Linnaeus ab. **nigrescens** ab. nov.

All parts of the moth, head, thorax, wings, and abdomen, are unicolorous blackish brown.

Type ♀: N. Kent, vii. 1910, L. W. Newman (Bright Coll.) Rothschild Coll.
Paratype ♀: loc. incog. (Bright Coll.) Rothschild Coll.

COSSIDAE

Zeuzera pyrina Linnaeus ab. **confluens** ab. nov.
Plate 1. fig. 6.

The spots in the cell of the forewing, in the interneural spaces beyond the cell, and along the inner margin, are more or less confluent. The spots on the hindwing may be confluent also.
Type ♀: London, J. A. Clark (Bright Coll.) Rothschild Coll.
Paratypes 3♀: 1♀; loc. incog. (Bright Coll.) Rothschild Coll.: 1♀; loc. incog. (Bond Coll.) R. Adkin Coll., mentioned in Barrett, *Brit. Lep.* **2**: 144.: 1♀; South Norwood, D. C. Goldthwait (Bright Coll.) Rothschild Coll.

PLATE ONE

Fig. 1. *Hepialus humuli* ssp. *thulensis* ab. *fumosa.* ♂. Type (White form).
Fig. 2. *Hepialus humuli* ssp. *thulensis* ab. *radiata.* ♂. Type.
Fig. 3. *Hepialus humuli* ssp. *thulensis* ab. *fumosa.* ♂. Paratype (Yellow).
Fig. 4. *Hepialus humuli* ssp. *thulensis* ab. *fumosa.* ♀. Allotype.
Fig. 5. *Hepialus humuli* ssp. *thulensis* ab. *radiata.* ♀. Allotype.
Fig. 6. *Zeuzera pyrina* ab. *confluens.* ♀. Type.

FLUCTUATIONS IN QUANTITY OF WORK ON BRITISH INSECTS

By BRYAN P. BEIRNE

Systematic Entomology Unit, Entomology Division
Canada Department of Agriculture, Ottawa

The majority of papers and notes published in the chief British monthly entomological periodicals are collecting or biological notes by amateur entomologists on British insects. Fluctuations in their numbers indicate broadly fluctuations in interest in the British insects.

The accompanying graph shows the total number of papers and notes published each year in *The Entomologist, The Entomologists' Monthly Magazine,* and *The Entomologists' Record.* The broken line shows the actual numbers, and the solid line the numbers calculated as three-year moving averages to reveal trends more clearly by smoothing minor irregularities. The numbers are for the calendar years, and corrections were made where the volumes, as published, did not coincide with calendar years.

The total number of titles in the three perodicals from 1865 to 1953 was about 55,000, or an average of about 624 per annum. The curve shows that published items were below this average for the 24 years up to and including 1889, much above the average for the next 22 years up to and including 1912, below average for the next 31 years up to and including 1944, and above average since 1945. The steady increase since 1938 is worth noting. More items appeared in the three periodicals in 1952 than in any other year since 1902. However, the increase becomes less striking when the population increase is taken into account. In relation to the population, about as many people published in 1871 and in 1947. On the same basis about two and a half times as many people were active entomologists in 1891 as in 1871 or 1947, and over three times as many were active in 1891 as in 1931. Though the relative increase in interest in recent years is not so great as the curve indicates, a definite upward trend has existed for the past 15 years and is apparently still in progress.

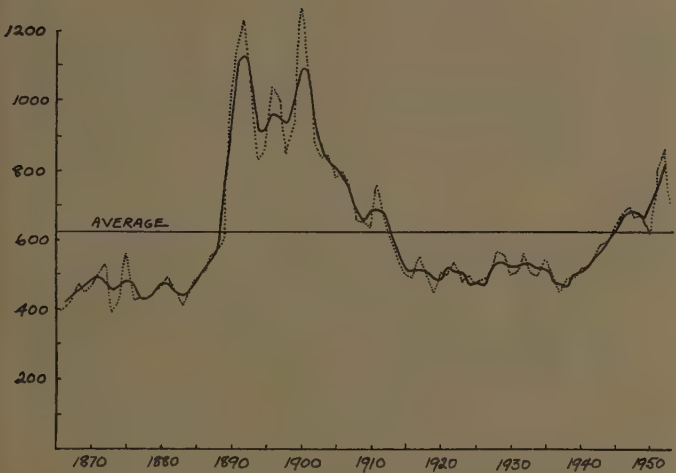
The graph shows three periods of increasing interest in British insects: between 1860, or earlier, and 1870; between about 1884 and 1892; and from 1938 onward. There was one main period of decreasing interest, between about 1900 and 1915. Incidentally, the establishment of new periodicals was a result, rather than a cause, of each period of increase. In each instance the periodicals were established after the increases had started: *The Entomologist* and

The Entomologists' Monthly Magazine in 1864, *The Entomologists' Record* in 1890, and *The Entomologists' Gazette* in 1950.

Apart from the conclusion that wars and economic depressions have had no significant effects, discussion on possible causes of fluctuations in the numbers of published items must be largely speculative. The increases in interest in the 1860's and 1890's may have been a result of the general interest in natural history that developed early in the nineteenth century, delayed because insects were considered less sensible and respectable objects for study by gentlemen than other natural history objects such as flowers, birds, or shell. The influence of Darwin's work (1859) may have stimulated interest in the 1860's The teaching of science subjects in the schools may have contributed to the increasing interest of recent years. The activities of amateurs may have been stimulated by the 'good' years for Lepidoptera that occurred in the 1890's and depressed by the successions of 'bad' years of the 1870's and 1920's. The decline in numbers of published items early in the present century may have been caused partly by a decline in the numbers of new locality records as the fauna became increasingly better known. In Ireland, where most captures are still worth recording, there was a major peak in the numbers of published items in the 1930's (Beirne, *Irish Nat. J.*, 1947, p.81).

The basic causes of fluctuations in interest were probably changes in mental outlook. Certain conditions favour interest in the subject by amateurs. For amateurs to exist in any country at any time the general standards of living and education must be high. In those parts of the world where these standards are low, entomologists, other than professionals, are few They were few in Britain 200 or more years ago. For amateurs to exist in any numbers economic and social conditions must be relatively stable. Leisure must be available for hobbies. Conditions of rapidly expanding economy, such as still exist in countries of North America and as existed in Britain at the time of the industrial revolution, result in the use of leisure for making or spending money rather than for materially unproductive intellectual pastimes such as entomology.

I wish to thank Miss H. R. Hollinsworth, Assistant Technician, Systematic Entomology Unit, Ottawa, for assistance in compiling the figures from the periodicals.



Total number of papers and notes published annually in *The Entomologist, The Entomologists' Monthly Magazine,* and *The Entomologists' Record*. Broken line: actual annual figures; solid line: annual figures calculated as three-year moving averages.

A NEW BRITISH SPECIES OF AGROMYZIDAE (DIPTERA)

By G. C. D. GRIFFITHS

On the 5th of September, 1953, I collected some Agromyzid puparia from *Glyceria maxima* (Hartm.) Holmb. at Ash Vale, Surrey, when attending the field meeting of the South London Entomological and Natural History Society. These were mostly the common *Agromyza nigripes* Meigen, but included three of entirely different shape. These have subsequently proved to be a remarkable new Agromyza species, which I now have the privilege of describing.

Agromyza distorta sp. nov.

Head (Fig. 1)

Frons narrowing anteriorly; in front view 2½ times the width of an eye, 2 times near the antennae, at the vertex as wide as its length from there to the antennae. Lunule very narrow, 1/5 of the distance of the frons from the front ocellus to its highest point. The shining pointed ocellar triangle reaches about as far as the 1st ors. The ocelli form an equilateral triangle. *Chaetotaxy:* 2 ors (an abnormal third on left side); 3 ori, the front pair shorter and positioned more inwards. Orbital setae in 1 row, directed upwards, reaching 2nd ors beyond the middle of the frons, nearer the 1st ori than the 1st ors. The oc pressed down, reaching past the 1st ori. Frons and cheeks visible before the eyes in profile. Jowls at the centre 1/7 of the perpendicular diameter of the eye, 1/5 posteriorly. About 5 peristomal bristles, vi strong, above it an additional hair and (further out) 2 to 4 cheek-bristles. Face in front view somewhat broader than high, median keel broad, flattened. Cheeks at the middle of the face almost as wide as the 1st antennal segment. Antennae with the 3rd segment widened towards the end (*nigripes* type), flattened on the fore-margin. Arista with pubescence similar to related species. Eyes clearly haired.

Thorax.

4 + 1 dc, becoming much shorter forwards; 5th dc nearer the suture than the 4th. Acr in 8 rows, almost reaching the 1st dc. Post-sutural ia in about 5 rows. 3rd dc before the sa; prsc strong. l.pa half as long as e.pa. Mesopleuron on upper and hind margins more thickly and roughly haired than in related species.

Abdomen

Last ♂ tergite somewhat longer than the penultimate; tergites approximately uniformly haired.

Legs

Ta with 2 conspicuous posterodorsal bristles.

Wing (Fig. 2)

The c reaches m_{1+2}. The ratio between the costal segments 2:3:4 is 3:1:2/3. R_5 clearly curved, diverging from m_{1+2} at its extremity. Last segment of m_{1+2} $3\frac{1}{2}$ times the length of the penultimate; last segment of m_4 almost $\frac{1}{2}$ the length of the penultimate; tp from beyond the middle of Cd to 5/8 of the same. Length of wing 2.5 mm.

Colour

Completely black; ocellar triangle and the or bases shining; face greyish dusted. Labial palps brown. Mesonotum faintly matt, without grey dusting. Abdomen somewhat more strongly shining. Legs all black, including the tips of the front femora. Wing veins brown, darker basally. Halteres whitish-yellow, squamae with black margin and fringe.

The new species runs to couplet 15, p. 95 in Hendel's (1938) key. It may be distinguished as follows:

15 Stirne von der Scheitelkante bis zur Fühlerwurzel gemessen so lang wie oben breit oder kürzer, oben $1\frac{1}{2}$-$2\frac{1}{2}$ mal so breit wie ein Auge 15a

— Stirn länger als breit, oben nur ca.ein Auge breit 17

15a Schüppchen tiefschwarz gewimpert. Augen deutlich behaart ....*distorta* sp. nov.

— Schüppchen weiss bis ockergelb gewimpert. Augen nicht merglich behaart 16

Holotype ♂: Bred from a puparium found attached to a leaf of *Glyceria maxima* (Hartm.) Holmb., at Ash Vale, Surrey, 5th September, 1953. Imago emerged 18th May, 1954, subject to the temperature of an unheated indoor room. It is in my collection.

The only adult specimen in existence at the moment is the type, but further puparia have been obtained this year and the larval stage located. Prof. M. Hering will describe this separately in his series in 'Tiidschrift voor Entomologie.'

The mine does not appear to differ from that of *Agromyza nigripes* Meigen, although the larva is entirely different. Prof. Hering informs me that the larva appears to have as many as 60 spiracular openings on the front spiracles (the previous maximum for the genus being about 20). These also give the puparia an entirely unique shape. Fig. 3 gives a general idea of their shape; the details of the spiracles, etc., will be covered in Prof. Hering's forthcoming description of the larva.

I am grateful to acknowledge Prof. E. M. Hering's generous assistance in the preparation of this paper.

REFERENCE

HENDEL, F., 1938. Agromyzidae, in LINDER E., *Die Fliegen der Palaearktischen Region.* 6(2).

13 Woodlands Avenue, Finchley, N.3.

5th October, 1954.

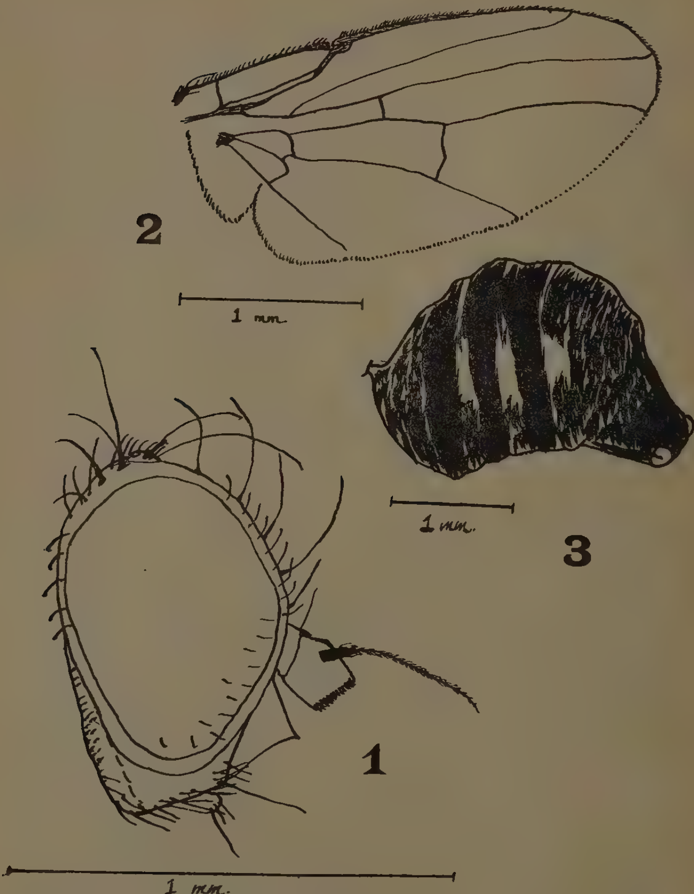


Fig. 1, Head in profile. Fig. 2, Wing. Fig. 3, Puparium in lateral view.
AGROMYZA DISTORTA sp. nov. ♂.

THE EGG AND MATURE LARVA OF *AESHNA ISOSCELES* (*MUELLER*) (ODONATA: AESHNIDAE)

By A. E. GARDNER, F.R.E.S.

Aeshna isosceles (Müll.) is a rare dragonfly and in the British Isles is confined to the area of the Norfolk Broads. Although mainly a Mediterranean species, it is found in central Europe as far east as Poland and Russia. It has an outpost in South Sweden and occurs sporadically in North Africa, Asia Minor and Turkestan.

Prior to 1952 the larva had not been found in Britain, and our knowledge of this stage, therefore, is meagre. Cabot (1881) figured the adult larva (reproduced by Popova, 1953), but the figure bears little resemblance to the actual insect. Lucas (1930) figures the labium and gives a brief description of the larva, this based on the examination of three exuviae lent by Dr. F. Ris, which were taken at Mettmenhaslersee, Switzerland, on 5th June, 1908. Schmidt (1936 and 1950) has further contributed to our knowledge and accurately figures the labium, abdominal spines and anal appendages.

After several abortive attempts I was fortunate in dredging up a single immature male larva of *Ae. isosceles* from a tangled mass of weed in a dyke at Potter Heigham, Norfolk, on 30th May, 1953. The larva was 20 mm. in length, generally dark brown in colour, with the first three abdominal segments pale yellowish—coloration which appears to be exhibited by all British Aeshnines during the early instars. Ecdysis took place on 3rd June, the abdominal coloration being uniformly brown, and the anal appendages so distinctive that identification was positive. Further moults took place on 3rd July, 5th August, and the final larval instar 26th September. Attempted emergence of the imago took place on 5th June, 1954.

Female imagines were observed on 24th June, 1950, and 27th June, 1952, at the Potter Heigham locality. They were seen to insert their eggs in the leaves and stems of *Potamogeton*, generally working backwards until nearly the entire length of the abdomen was submerged. One female was seen ovipositing in the upright stem of a sedge above the surface of the water. A female captured on 27th June, 1952, was induced to oviposit in the rotting leaves of *Potamogeton* on 30th June. The eggs hatched on 5th August, 1952,* but the young larvae failed to survive beyond the 3rd instar. It would appear that *Ae. isosceles* requires two years to reach maturity, that it may be classified as a spring species, having no diapause in the egg stage,

* Published in error as '1953' in *Proc. R. ent. Soc. Lond.* (*C*), 1953, **18**: 44, and *Ent. Rec.* 1953, **65**: 359.

but a faculative diapause in the final larval instar. These characteristics are shared by *Brachytron pratense* (Müll) (Münchberg, 1930), and *Anax imperator* Leach (Corbet, unpublished).

Egg (Fig. 5)

Only two eggs were available for examination; this description, therefore, is considered tentative, but perhaps desirable, as no published description appears to have been made. Length 1.56-1.71 mm., greatest width 0.31-0.39 mm., which occurs at the apical third. Anterior pole terminating in an obtuse pedicel. Extreme anterior portion of the chorion bearing hexagonal markings, which become ill-defined and finally inevident. In this respect the eggs resemble those of *Ae. mixta* Latr. (Gardner, 1950), rather than those of *Ae. cyanea* (Müll.) (Gardner, 1951), in which species the cell-like markings extend down the entire length of the egg. There is a suggestion of a blade-like extension anteriorly, but markedly less evident than that of *Anax imperator* (Corbet, unpublished). This character may be anticipated as the eggs of both species are non-diapause and are inserted in similar aquatic plants.

Final Instar Larva (Fig. 1) ♂.

Colour

General coloration light brown, with darker marblings; ventral surface uniformly pale. A more detailed description of the coloration is given under the separate headings.

Length

Excluding the antennae, but including the anal appendages, 42 mm. Greatest width 8.89 mm., which occurs across the eyes. Lucas gives the length as 40-42 mm., and width as about 9 mm.

Antennae

These are comparatively short, set 2.40 mm. apart, and consist of 7 segments, of which the 1st (basal) segment of the flagellum is markedly the longest. Total length 3.07 mm. *Toruli:* Conspicuous, dark brown in colour, anterior lateral margins bearing a dark suffusion. *Scape:* Length 0.23 mm., outer margin straight, inner margin convex in outline. *Pedicel:* Length 0.34 mm., barrel-shaped, bearing uniformly spaced piliform setae. Both scape and pedicel are light brown in colour. *Flagellum:* Slender, pale, the relative width of each segment becoming progressively less to the slender and pointed apical segment. All segments bear scattered trichiae down the greater part of their length in addition to the apical crowns. Length: 1st (basal), 0.87; 2nd, 0.34; 3rd, 0.42; 4th, 0.40; 5th (apical), 0.47 mm.

Eyes

Large, somewhat hemispherical in lateral outline and dorsally flattened. They are golden brown in colour, darker towards their inner margin and on the prolongations, the latter not markedly directed caudad towards the median epicranial suture.

Ocelli

Median ocellus indicated by a prominent pale yellowish area triangular in outline. Lateral ocelli small, pale, inner margin bordered by a prominent black triangular suffusion.

Head

Transverse in outline, dorsally flattened. Length from the anterior margin of the only slightly protruding labium to the concavity of hind margin 4.81 mm. Width over eyes 8.89 mm. Vertex slightly raised, frons and clypeus hemispherical in outline, strongly produced, pale mid-dorsally, the posterior area of the frons marked with a pale lateral spot. Occiput with the lateral margins of the postocular lobes nearly straight, then gently curved to the wide and moderately deep concavity of the hind margin. The pale median epicranial suture is enclosed by a dark and slightly raised immaculate pear-shaped ridge, this being flanked by a kidney-shaped area of similar nature, the anterior portion of which bears a small circular spot. The lateral margin of the postocular lobes are dark, are flanked by a pale crescent-shaped band which shows up conspicuously from the medium brown tint of the more central area of the occiput, which bears dark longitudinal striations. The slightly raised ridge bordering the posterior margin of the eye prolongations bears an oblong pale mark at about mid-length. A field of short setae border the hind margin of the occiput, these increasing in length on the extreme margin.

Labium (Fig. 2)

Prementum: Somewhat flattened, median area depressed, median sulcus long and narrow. Length 6.37 mm., reaching to the insertion of the mid-legs; greatest width 5.16 mm., which occurs anteriorly, width at base 2.48 mm. Distal margin of median lobe moderately produced, thickly fringed with piliform setae; median cleft slit-like and extending for 0.45 mm. Lateral margin strongly convex anteriorly, armed with closely set short setae; at about mid-length tapering to the labial suture, armed with scattered short spiniform setae. A field of spiniform setae are situated slightly inward and at the base of the anterior convexity. *Labial palpi:* Outer margin convex, slightly angled; inner and distal margins straight and serrated, outer distal angle rounded, end hook obtuse. Movable hooks 2.04 mm. in length, curved, and armed with irregularly spaced piliform setae along almost their entire length. A field of spiniform setae of moderate length are situated proximal to the base of the movable hooks. Ventral surface of labium immaculate.

Cervix

Collar-like, pale mid-dorsal area flanked by a dark suffusion.

Prothorax

Correlated with the cervix, somewhat bell-shaped in outline. Length 1.85 mm.; greatest width, which occurs just above the posterior transverse carina, 5.55 mm. The pale and slightly raised mid-dorsal area

flanked by a longitudinal dark suffusion which extends nearly to the posterior lateral margin. Surface covered with minute dark points, these being the darkly pigmented seatings of short setae, a tuft of piliform setae situated on the outer lateral margin.

Synthorax

Length measured at the lateral margin 6.48 mm.; greatest width 7.03 mm., which occurs at about mid-length. Generally of a uniform light brown tint, with darker suffusions; both the meso- and meta-pleurae bear two pale and oblong spots on the dorsal surface towards the inner margin. Dorsal and lateral surface covered with dark points.

Wing-sheaths

Held parallel, hind overlapping the fore. Length 10.37 mm., the hind extending to the bottom of the 4th abdominal segment. Margins armed with short piliform setae. Pale brown in colour, at maturity the imaginal wing venation being distinct and dark brown in colour.

Legs

Of moderate length, of a uniform light brown colour, the femora bearing two ill-defined transverse bands apically. Length of the leg parts in millimetres:

	Femora.	*Tibiae.*	*Tarsi.*	*Claws.*	*Totals.*
Fore	4.81	5.18	2.62	0.40	13.01
Mid	5.55	6.11	2.62	0.40	14.68
Rear	6.29	6.48	2.92	0.55	16.24

The coxae and trochanters add about 1.85 mm. to the extreme reach of the legs when fully distended.

The tarsi may be further tabulated as follows:

	Basal segment.	*Middle.*	*Apical.*	*Totals.*
Fore	0.18	0.96	1.48	2.62
Mid	0.18	0.96	1.48	2.62
Rear	0.33	1.11	1.48	2.92

Chaetotaxy: Femora armed on the inner and outer margins with closely spaced short spiniform setae; similar setae occur on the arched dorsal surface and are most numerous on the fore femora. *Tibiae* armed with irregularly spaced piliform setae on the outer margin; apical combs consisting of tridentate setae most numerous on the anterior ventral surface of the limb. On the inner margin they extend downwards for only a short distance and are then replaced by simple setae to nearly the base of the tibiae. *Tarsi* armed with closely set, slender tridentate setae, which occur along the inner and outer margin of the ventral surface of each segment. *Supracoxal armature* (Fig. 3) fairly distinctive in outline, the anterior lobe being more slender and markedly shorter than the posterior lobe.

Abdomen

Moderately stout, not markedly contracted basally, dorsally convex. Length (excluding anal appendages) 22.96 mm.; greatest width

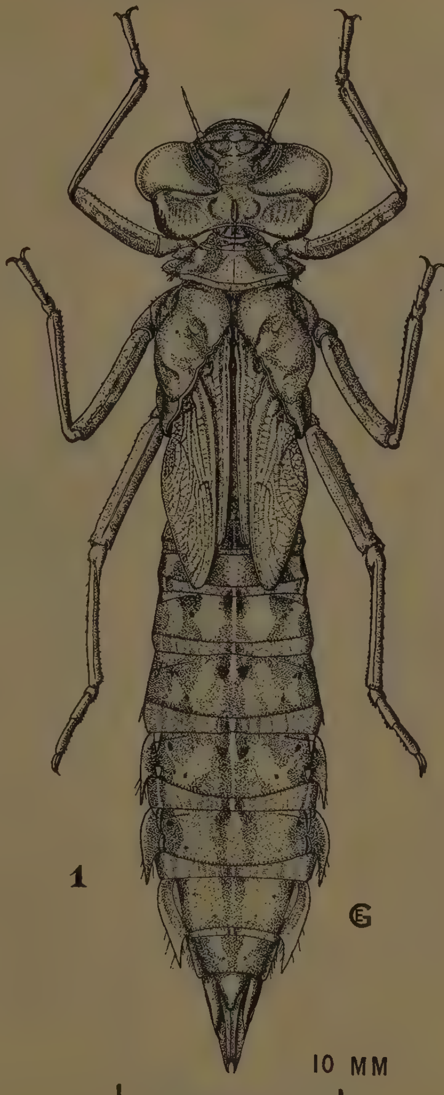
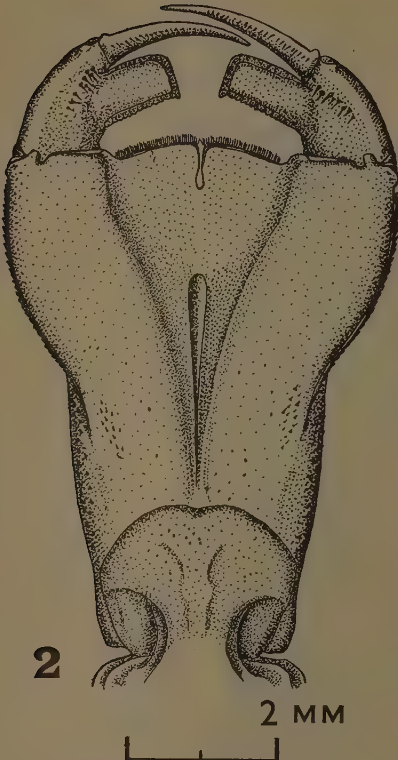


Fig. 1, Mature larva ♂. *AESHNA ISOSCELES (MUELLER).*



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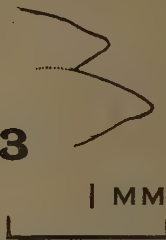

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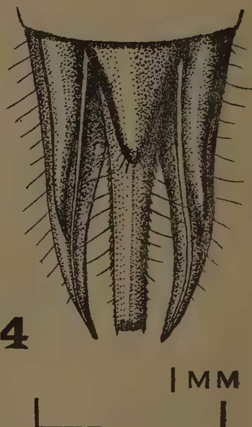

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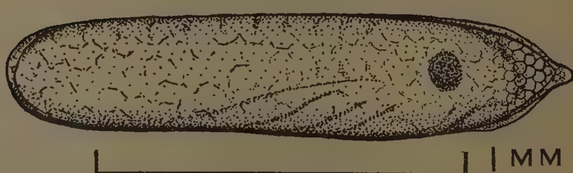

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Fig. 2, Labium. Fig. 3, Supracoxal armature. Fig. 4, Anal appendages ♂. Fig. 5, Egg.

AESHNA ISOSCELES (MUELLER).

8.15 mm., which occurs at the 8th segment. Lateral spines on segments 6 to 9. Those on 6 short, slender and not very evident when viewed dorsally; those on 7 slender, reaching nearly to the base of the 8th segment; those on 8 conspicuous, slightly incurved, reaching to just below the base of the 9th segment; those on 9 broad basally, slightly incurved, reaching nearly to the apex of the 10th segment. All spines bearing marginal piliform setae, which attain greatest length on the apical margins. Posterior margin of all segments bearing short spiniform setae, these most prominent on segments 7 to 10. *Colour:* Generally of a light sepia tint, dorsal and ventral surface bearing numerous dark points as described for the prothorax. The pale mid-dorsal line at the base of segments 4 to 7 is flanked by a dark band, which becomes slightly less evident on segments 8 to 10. The dorsal puncta are surrounded by a conspicuous black suffusion on segments 4 to 7, less so on 8, and become inevident on 9 and 10. Submedian band pale, irregular in outline, indefinite on segments 8 to 10. Lateral margin, with darker marblings, irregular in outline. Lateral and dorso-lateral puncta fairly conspicuous on segments 4 to 7, less so on 8, inevident on 9 and 10. Posterior transverse carinae conspicuously marked with pale fasciae.

Anal appendages (Fig. 4)

Epiproct: Length 3.6 mm., apical half narrow, parallel, distal margin nearly straight. *Male projection:* Prominent, triangular, length 1.55 mm. *Paraprocts:* Length 4.10 mm., slightly incurved, apically pointed. *Cerci:* Distinctive, slender, apically incurved, 2.96 mm. in length. They are approximately two-thirds the length of the paraprocts and serve as the most distinctive separation character for this species. Apices of paraprocts, epiproct and cerci dark, as is also the lateral margin of the male projection. Lateral margins of the epiproct and paraprocts armed with long, dark and piliform setae.

Separation characters

Even in the field the long cerci will readily distinguish this species from other species of British *Aeshna*. The almost straight distal margin of the epiproct and the outline of the supracoxal armature serve as supplementary characters.

Acknowledgments

I am indebted to Miss C. Longfield for assistance with the literature, and to Dr. P. S. Corbet for kind permission to refer to his unpublished observations on the egg of *Anax imperator*.

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NATURAL FLUCTUATIONS IN ABUNDANCE OF BRITISH LEPIDOPTERA *

By Bryan P. Beirne †

1. INTRODUCTION

Information on the extent, frequency, and causes of changes in the abundance of Lepidoptera in the British Isles was compiled from the available literature during the course of studies on the origin and history of the British macrolepidoptera (Beirne, 1947, 1952). The following is an attempt to summarize the information on some aspects of this and to arrive at some general conclusions on the relative importance of various control factors. The discussion may serve to indicate the nature of useful observations that are probably made far more often than they are recorded.

Natural control factors discussed here are those that have been recurrent. Over periods of thousands of years the effects of some of them have been persistent or permanent and have regulated the present distributions of many species. However, within the past century, the period covered by published records of observations, their effects were usually temporary. In this way they differ from non-recurrent control factors, whose effects were usually persistent or permanent. The latter include, for example, human activities that affect Lepidoptera directly or indirectly, and intrinsic changes in the species that result in reductions, without apparent external causes, in reproductive vigour or in egg fertility.

It is not practical to list each of the several thousand references consulted. Consequently references are omitted when well-known facts are quoted and when the annual abundance of the Lepidoptera as a whole is described. There is doubtless additional information in the publications of some local societies that were not available for consultation.

2. ACKNOWLEDGMENTS

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3. FLUCTUATIONS IN ABUNDANCE OF LEPIDOPTERA

With a very small number of exceptions, such as *Sedina büttneri* Her., each species of Lepidoptera inhabits the British Isles as a number of populations, that is, of interrelated groups of individuals that

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are more or less clearly isolated from other groups. The great majority of species are each represented by a large number of populations, though in a few generally distributed and very common species, such as *Triphaena pronuba* L., the populations are so confluent as to be in effect one or a few very large populations. Every population varies from time to time in the number of individuals that comprise it. This variation is both apparent and real. Apparent, but not necessarily real, reductions may be indicated by the relatively small numbers of individuals seen or captured when conditions are unfavourable for their activities. The numbers seen or captured when conditions are favourable, for example, on a 'good' night for moths, indicate more accurately the real relative densities of populations than captures on 'average' or 'bad' nights. There also may be apparent, but not necessarily real, reductions when the efficiency of a collecting method is offset by opposing natural attractions. The relative scarcity of noctuids at artificial baits when honeydew or flowers are abundant nearby is a familiar example.

There are some thousands of published descriptive records of fluctuations in population densities. These indicate fluctuations that often range from conditions when few or no specimens are seen in a locality for several years to conditions of great abundance for the same species there. Statistical data are relatively few. However, figures given by Banerjee and French (1952) for 17 species captured in light traps in eight years show differences in the numbers between the year of greatest abundance for a species in one locality and its year of greatest scarcity there that range from 2.1 times, for *Spilosoma lubricipeda* L., to 66.6 times for *Agrotis exclamationis* L., with an average of 11.4 times for the 17 species. Figures for less common species are often more extreme. Usually this does not necessarily or probably indicate more extreme real fluctuations. They may be the result of minor distributional changes—the movement of the main breeding-site from one part of a habitat to another, and consequently nearer to or farther from the collecting-site—combined with annual fluctuations in population densities.

Outbreaks, that is, excessive local abundance of species, occur primarily with species whose normal level of abundance is high, with species whose food-plants grow in large areas of more or less pure stands, and with species whose habits are such that there is a tendency for a heavy population of larvae to build up in a limited area. Outbreaks of species whose normal level of abundance is high and which normally occur as large populations may cover relatively large areas. For example, *Triphaena pronuba* L. is normally a very common species, but occasionally, as in southern England in 1881, it becomes excessively abundant over large areas. The normal mean level of abundance varies with the locality and region. For example, in many parts of southern England *Tortrix viridana* L. is normally very abundant, whereas in Ireland it is normally merely common.

Outbreaks occur with some species whose habitats are limited in vegetational composition, and therefore in variety of animals that may be natural enemies of the species. Examples are *Charaeas graminis* L., *Philudoria potatoria* L., and *Macrothylacia rubi* L., outbreaks of which occur mainly on hill pastures. More often, outbreaks occur where large areas of the food-plant have developed rapidly either from planting by man or after some catastrophe. Examples of the latter are the great increase in many species that followed the sudden and extensive development of their food-plants on bombed sites in London (Owen, 1951) and the increase of *Hadena chenopodii* Schiff. that followed the great increase of its food-plant, *orach*, when the sea receded from the Horsey Mere area after the great flood of 1938 (Ellis, 1938). Outbreaks such as these result when a population of a species is initially able to increase more rapidly than those of its parasites and when unfavourable direct control factors are negligible. A further cause of outbreaks is that some species can spread into new areas of food-plant more rapidly than their chief parasites. This has occurred with, for example, *Pieris brassicae* L., and *Agrotis segetum* Schiff., species that are known to migrate considerable distances and that occasionally reach outbreak proportions in cultivated areas.

Species whose habits are such that there is a tendency for heavy populations to build up in limited areas have outbreaks that normally are very limited in extent. Outbreaks of these that cover larger areas may be in fact composed of a large number of small outbreaks sufficiently close together to become more or less confluent. The species in question are either those whose females are flightless, so that the eggs must be laid in a limited area, for example, *Orgyia antiqua* L., *Operophtera brumata* L., *Phigalia pedaria* Schiff., *Erannis defoliaria* Cl., *E. leucophearia* Schiff., *E. aurantiaria* Esp., and *Alsophila aescularia* Schiff.; or species that lay their eggs in batches and whose larvae are gregarious, at least in the earlier instars, for example, *Euphydryas aurinia* Rott., *Euproctis phaeorrhoea* Don., *Malacosoma neustria* L., *Eriogaster lanestris* L., and *Yponomeuta* spp. It seems likely that the temporary relaxation of a natural control factor that normally operates at a critical stage in the life-cycle—perhaps predator attack on the flightless females or on the colonies of larvae—may be responsible for outbreaks.

The absence or relaxation of natural control factors that usually operate at critical periods in the life-cycle also appear to be responsible for the more or less localized outbreaks of other species. For example, rain can cause heavy mortality to newly hatched larvae of *Tortrix viridana* L., which may explain why this species is normally less abundant in Ireland, where rain is frequent, than in southern England; and rain apparently is very detrimental to the larvae of *Agrotis segetum* Schiff., and other cutworms, which consequently can reach outbreak proportions only in dry seasons.

In addition to fluctuations in the abundance of individual species,

there are fluctuations in the abundance of adult Lepidoptera as a whole, that is, more or less simultaneous similar variations in the densities of populations of a large number of species, often including all or most of the populations of those species over wide areas. This fact is well known to collectors, who term a good year one in which Lepidoptera as a whole are exceptionally common, and a bad year one in which they are abnormally scarce (applied entomologists use the terms in the opposite senses). There are many descriptive records of good and bad years, and in recent years some numerical data have been published for individual localities. The numbers of specimens captured in light traps operated continuously ranged from 13,182 to 40,023 per annum in four years (Williams, 1939), were 2,921 and 6,801 in two years (Best, 1950), and 9,824 and 16,770 in two years (Bell and Bell, 1946), and, for the ten most common species, ranged from 1,911 to 3,658 in three years (Bell and Bell, 1948); the number of butterflies seen in three years ranged from 5,434 to 20,852 per annum (Stallwood, 1950), the numbers of moths seen at rest on a fence from January to March of seven years ranged from 23 to 178 per annum (Crauford, 1951), and the number of specimens of moths seen in six months of each three years ranged from 145 to 369 per annum (Evans, 1950).

The majority of individuals are, of course, of a relatively few common species. For example, of a minimum total of 15,400 moths at sugar on 251 nights in eight years 55 per cent were of six species and 74 per cent of 12 (Hodgson, 1947). Nevertheless, it is evident both from statistical data and descriptive records that in a good year a considerable number of species, though not always a majority, are above their mean levels of abundance. Of 143 species of which ten or more specimens were captured in light traps in at least one of four years by Williams (1939), the largest number, 70, were at their year of maximum abundance in the year when the total number of captures was highest, and only four were at their maximum abundance in the year when the total was lowest.

Analysis of descriptive records suggests that no two good or bad years have been identical in respect of the species that were abnormally abundant or scarce. In general, species that were unusually common or unusually scarce in any one year tended to have something in common in habits or life-history. This, as will be apparent from examples quoted later, is because some important factors that result in decreased or increased abundance tend to affect in the same ways species that have similar habits or that are in the same stage of the life-cycle at the same time. On the basis of the descriptive records, in most good years some species were scarcer than normally, and in some bad years some species were unusually numerous. Figures given by Banerjee and French (1952) further show that years of maximum abundance of individual species do not necessarily coincide: in eight years of light-trapping there was only one year in

which none of the 17 most common species was at its maximum abundance, and only one in which none was at its minimum, and in any one year not more than five of the 17 were at their maxima and not more than six at their minima.

The only evidence on which the relative abundance of Lepidoptera as a whole over wide areas can be estimated at present is provided by descriptive records. From analysis of the recorded opinion impressions may be gained on the characteristics of each year since 1864 in so far as the relative abundance of the Lepidoptera as a whole in the British Isles is concerned. Reasonably accurate estimations can be made for the period from about 1881 to 1901, because of the large numbers of records for those years, but the period from 1864 to about 1874 and, more especially, that from 1920 onward are very inadequately documented, and the estimations for years in those periods are often largely guesswork and consequently not necessarily reliable. The characteristics of each of the years since 1864, in respect of the relative abundance of Lepidoptera as a whole, seem to have been as follows:—

1864: apparently about average; 1865: apparently better than 1864, with butterflies abundant; 1866: bad; 1867: bad; 1868: good after a poor spring; 1869: bad, but good for larvae; 1870: apparently good after a poor spring; 1871: about average; 1872: apparently bad; 1873: possibly bad; 1874: average or below; 1875: apparently average; 1876: apparently average; 1877: apparently average or below; 1878: bad; 1879: bad; 1880: bad or possibly average; 1881: very good; 1882: bad, especially for macrolepidoptera with arboreal larvae; 1883: bad for macrolepidoptera, but average or better for microlepidoptera and apparently above average in Ireland; 1884: bad except in south-east England; 1885: above average; 1886: average or below average; 1887: above average and good for butterflies and microlepidoptera; 1888: good, but some deterioration in late summer and autumn; 1889: bad, but not so bad in spring; 1890: bad; 1891: varying with the region, but in general better than 1890 and good for larvae; 1892: very good for both larvae and adults, and a remarkable year for butterflies; 1893: good in spring, but later becoming bad except for many butterflies; 1894: bad; 1895: generally below average, but good in the spring and in the north and west; 1896: below average, but not so bad in the spring; 1897: varying with the region, but in general about average after a bad spring; 1898: average; 1899: good, particularly for butterflies, after a bad spring; 1900: rather good after a bad spring; 1901: average or above average; 1902: bad, but some larvae abundant; 1903: bad, but improved in late summer and autumn; 1904: bad; 1905: good, but deteriorated in late summer and autumn; 1906: above average, and good for butterflies; 1907: bad, especially in autumn; 1908: apparently above average; 1909: bad, but spring larvae very abundant; 1910: bad;

1911: apparently good after a bad spring; 1912: in general average or below, but in spring above average; 1913: bad; 1914: above average after a poor spring; 1915: possibly above average; 1916: average or below, but spring larvae common; 1917: good, especially for butterflies; 1918: good, especially for butterflies and spring larvae; 1919: below average.

1920: Below average; 1921: average, but good for butterflies; 1922: average; 1923: below average; 1924: bad, but autumn larvae common; 1925: bad; 1926: below average; 1927: below average; 1928: average or slightly above; 1929: average; 1930: above average; 1931: bad; 1932: apparently above average after a bad spring; 1933: good, especially for butterflies; 1934: good, but not as good as 1933; 1935: apparently above average except in early summer; 1936: apparently average or below; 1937: average, but below average for butterflies; 1938: apparently average or below average; 1939: apparently above average, especially in late summer; 1940: good; 1941: good after a poor spring; 1942: bad; 1943: apparently bad; 1944: apparently bad; 1945: apparently good; 1946: apparently about average, but better in the autumn; 1947: apparently good; 1948: apparently about average, but spring larvae abundant; 1949: apparently about average, but better in autumn; 1950: apparently below average after a bad spring; 1951: apparently average or below; 1952: apparently average or below.

Some tentative conclusions may be reached from the above estimations. Good years occurred singly or in twos, never in longer successions. There was about one chance in three that a good year would be followed by a second good year. The increase in abundance from bad to good was either rapid, from one year to the next, or gradual, over two, three or four years. The decrease following a good year or pair of good years was always rapid, from one year to the next. Isolated good years or the second of a pair of good years were usually followed by bad years and rarely by average years. Bad or average years were followed by bad, average or good years, but when a bad year was followed by a year that improved rapidly as it progressed, then the following year was usually good. Bad or average years did not tend to occur in successions of certain numbers: they occurred singly or in successions of up to 13 years. The relative abundance of Lepidoptera in the spring was not necessarily related to the abundance in the summer and autumn, and the relative abundance in any year was not necessarily related to the relative abundance of larvae in the preceding year. There are indications of a tendency for bad years to be followed by springs that were bad for Lepidoptera, and for good years to be followed by good springs. In this paragraph above-average years are, for convenience, treated as good years and below-average years as bad years.

Temporary fluctuations in the sizes of populations, either of individual species or of groups of species, result from variations in the

intensity of control factors. The number of eggs that can be laid by an individual female varies with the species, but with most is of the order of several hundred. Because of this, there is an inherent tendency for the numbers to increase very rapidly. This tendency is normally kept in check, within variable limits, by factors that cause mortality of all stages and that influence the extent of the breeding and egg-laying. There are also indirect factors that influence the incidence or intensity of the direct control factors. These must be considered in any discussion of the natural control, especially as some of them act both directly and indirectly.

4. NATURAL ENEMIES

a. Predators

It is often difficult to judge the relative importance of predators in the natural control, particularly predators that are not highly specialized in their feeding-habits. It is especially difficult to estimate the relative importance of predators in the natural control of those species of Lepidoptera that are not highly specialized in habits. Most of the important predators and most of the species of Lepidoptera—for example, those whose larvae are free-living on vegetation—fall into these categories. The chief reason for the comparative paucity of definite information is that such information has to be obtained by field observations, which are usually difficult because of the difficulty in identifying to species insects, particularly larvae, seen being eaten, and because it is difficult to identify to species lepidopterous remains found in the stomachs of predators.

However, the importance of predators in the control of those species of Lepidoptera whose larvae are free-living may be inferred from a number of indications. The rapid decrease in numbers of individuals from unknown causes has often been noted. For example, 96 of 100 pupae of *Aglais urticae* L., disappeared (Poulton and Sanders, 1898); 84 of 350 eggs of *Pieris rapae* L., disappeared (Richards, 1940); the number of eggs of the yellow sallow moths eaten by predators is 'often astonishing' (Allan, 1951). A local or seasonal scarcity of predators may result in a marked increase in the abundance of Lepidoptera. The most striking example of this is the increase that follows a severe winter, and that is attributed to decreases in the numbers of insectivorous birds; this is discussed more fully later. Conversely, if a species of predator becomes abundant a scarcity of species of Lepidoptera may follow. For example, a local scarcity of *Nyssia zonaria* Schiff. was attributed to the appearance of great numbers of plovers (Ivy, 1888); whole broods of larvae of *Aglais urticae* L., and *Nymphalis io* L., were wiped out by wasps in the great 'wasp year' of 1935, and adults of *Lysandra coridon* Poda and *Polyommatus icarus* Rott., were heavily attacked (Fletcher, 1936); and a local great scarcity of Lepidoptera was attributed to a great abundance of *Formica rufa* L., (Steuart, 1891). Finally, it is known that Lepidop-

tera, particularly larvae, comprise a major part of the food of many animals, notably insectivorous birds. For example, a pair of great tits consumed 8000 larvae in three weeks (Witherby *et al.*, 1938). The indications are that predators are a major factor in the control of most Lepidoptera, and the relative lack of definite records as compared with those of parasites does not mean that predators are necessarily less important than parasites in the broad picture.

Information is more exact where predator attacks leave identifiable traces. The traces may consist of the opened, empty mines of stem-boring larvae. For example, only two or three per cent of the larvae of *Aegeria culiciformis* L., which bores in trunks of birch, normally escape attack by woodpeckers and reach maturity (Reid, 1905); the mining larvae of most species of Aegeriidae are heavily attacked (Fassnidge, 1928; Jackson, 1948); considerably more than half the larvae and pupae of *Argyresthia laevigatella* H.-S., which mines shoots of larch, are eaten by birds (Irvine, 1911; Beirne, 1942); and over 80 per cent of the pupae of *Nonagria cannae* Ochs., in stems of bulrush, are normally eaten by birds (Edelsten, 1899). The traces may be dead adults, for example, in spiders' webs or in leaves of sundews; discarded wings, as with specimens attacked by bats; beak-marks on wings, as with specimens that were attacked by birds but escaped; opened cocoons or paralysed or dead larvae in nests of the predators, as with wasps of *Ammophila*, *Odynerus*, and related genera.

There are a number of records of attacks by predators on Lepidoptera in Britain where either or both predator and prey were identified; these records indicate identities of predators. Birds appear to be the most important of the vertebrate predators. They attack all stages, particularly the larvae. Following a survey of oakwoods in the Clyde area it was concluded that birds were having a significant effect on the population of defoliating larvae (Brian and Brian, 1950). Bats are important predators of the adults of nocturnal species. Wasps that provision their nests with larvae may be primary natural control factors of some species, but little information is available. In one locality *Ammophila sabulosa* L. apparently was the chief factor that controlled *Nyssia zonaria* Schiff., on whose presence the survival of the sandwasp depended (Stelfox and Stelfox, 1937).

Other kinds of predators may be important, but records are too few or inadequate for their importance to be judged. Moles may be important in the control of species with subterranean larvae or pupae. Mice and voles may cause greater destruction to larvae, pupae and adults than the fewness of the records indicates. It may be significant that some major outbreaks of *Charaeas graminis* L. occurred in almost exactly the same areas where there had been major vole outbreaks a few years before. Predatory Hemiptera that attack eggs and larvae may be important in the control of many species, especially of those whose larvae are leaf-miners or leaf-rollers, but here, as with other predators, published records—of which there are a number—refer

to individual instances of attack. The significance in the natural control of the mites that sometimes infest adult Lepidoptera is not clear. It has been suggested that they may be detrimental to *Melanargia galathea* L., a species particularly liable to infestation, by impeding flight. It is possible that mites may be important egg predators. Carabid beetles, which attack adults and larvae, may be of some significance. One species was stated to have been of considerable importance in the control of defoliating larvae on oak (Cook, 1936), and there are a number of records of individual attacks.

Predators that, so far as can be judged from existing records, may be only casual natural enemies and that are apparently not normally of major importance to any species include frogs, toads, and hedgehogs, spiders, earwigs, dragonflies, sawflies. Orthoptera, and midges, centipedes, and snails, all of which have been recorded as attacking Lepidoptera in Britain. Sundews may be included here. Some kinds of predators appear to be normally unimportant as natural enemies of Lepidoptera, but may become important when they become abundant. Wasps and ants have been mentioned already in this connection, and other examples are hornets and predatory Diptera (empids and asilids).

In general the records indicate that predators are normally serious natural enemies of species that have specialized habits, for instance, species of Aegeriidae, whose larvae bore in branches of trees or shrubs, species of *Nonagria,* whose larvae bore in stems of bulrush or reedmace, and species of Hepialidae that have a specialised manner of flight—they fly slowly at a more or less uniform height—all of which undergo heavy destruction by birds. Most kinds of predators probably attack most species of Lepidoptera in proportion to their numbers in relation to those of other species in the same situation, though this must be considerably modified by the relative visibility of the different species to the different kinds of predators.

Predators often tend to congregate where Lepidoptera are most numerous. For example, outbreaks of larvae of *Tortrix viridana* L., attract flocks of rooks and other birds (Woodford, 1921; Raynor, 1885; Flintoff, 1931), and outbreaks of the adults have attracted numbers of male empids (Wood, 1858; Poulton, 1906; Goffe, 1934); attention has first been drawn to outbreaks of *Charaeas graminis* L., on isolated hill grasslands by the presence of flocks of birds attracted by the larvae (Service, 1894; Mitchell, 1936; Cameron, 1938); in 1935, when immense swarms of *Pieris brassicae* L., invaded the British Isles, adults were eaten in large numbers by birds; outbreaks of larvae of *Euproctis chrysorrhoea* L., *E. phaeorrhoea* Don., and *Lasiocampa quercus* L., whose larvae are not ordinarily eaten by birds, have attracted abnormal numbers of cuckoos (Owen, 1949), and a parallel instance with larvae of *Abraxas grossulariata* L., and meadow pipits is on record (White, 1935). The attraction of predators to a concentration of prey was illustrated experimentally by the libera-

tion of a large number of adults of *Taeniocampa gothica* Schiff., all of which were eaten by birds within half an hour (Harrison, 1936).

Lepidopterous larvae that have cannibalistic tendencies also tend to become important natural enemies of other species when the latter become abundant. In outbreaks of larvae an effect of the overcrowding is that larvae with cannibalistic tendencies, for examples, those of *Cosmia trapezina*, L., and *Eupsilia transversa* Hufn., tend to feed on other larvae rather than on foliage (Stowell, 1921).

Man has been an important predator of some species— particularly in that the greater the rarity of the species the greater its liability to attack. In this way man differs from other predators. Local scarcities or extinctions of some 40 species of Lepidoptera have been attributed to overcollecting. This figure includes 19 of the 59 permanently resident species of butterflies. Overcollecting has had serious effects on individual populations of Lepidoptera at certain times; *Lycaena dispar* Haw., and *Zygaena meliloti* Esp., are well-known examples of species that have suffered. However, its effects on the Lepidoptera as a whole, even with the extensive use of ultra-violet light-traps have often been over-estimated and probably have been and will be negligible as compared with the effects of other control factors.

Some examples may be quoted to illustrate how even minor differences in habits may influence strongly the incidence of predator attack. The hawthorn-feeding race of *Yponomeuta padella* L., spins its cocoons in groups, and the pupae are liable to heavy destruction by the predatory larva of a species of Diptera (Beirne 1943), and it is reasonable to assume that mortality from this cause is much less with the apple-feeding race of the same species which spins its cocoons singly; the eggs of young larvae of *Pieris rapae* L., on wild crucifers are more severely attacked by predators than are those on cabbage (Richards, 1940); *Melitaea athalia* Rott., becomes lethargic on alighting on flowers and because of this is readily captured by spiders, whereas more active butterflies on the same flowers largely escape (Stroyan 1950); *Pieris brassicae* L., in flight is attracted by resting specimens of the same species and, probably because of this, an estimated six million specimens were trapped by sundews in an area of about two acres (Oliver, 1944).

b. Parasites

Most, and probably all, British species of Lepidoptera are attacked in one or more of the early stages by hymenopterous or dipterous parasites, or by both. There are a few records of parasitism by nematodes. Parasitism by insects is frequently high. For example, there are records of 90 per cent or higher parasitism in larvae of *Anepia irregularis* Hufn., *Orthosia gracilis* Schiff., *Pieris brassicae* L., *Simyra albovenosa* Goeze, and *Plutella maculipennis* Curt. It has even been suggested that, because of attacks by parasites, *Pieris brassicae* L., might die out as a British species if it was not reinforced regularly by

immigrants from the Continent (Williams, 1949). Shepherd (1926) concluded that parasites were mainly responsible for periodical scarcities of a number of species of butterflies. More, and more definite, information is available on parasites than on predators and diseases, largely because parasites can be obtained and the minimum incidence of their attacks noted by rearing larvae and pupae collected in the field. However, because of the perennial difficulty in having parasites identified to species, the information is not as adequate as might be supposed.

There are a number of records of sudden decreases in the relative abundance following abnormally heavy parasitism. For example, all larvae of *Celastrina argiolus* L., collected in 1930 were parasitized, and the species, though normally common, was scarce in southern England in 1931 (Buckstone, 1931); and *Pieris* spp. were abundant in 1929 and their larvae caused much economic damage, but larvae of the second generation were heavily parasitized and, probably mainly as a result of this, attacks to crops were slight in 1930 (Fryer, 1933). There are records of groups of species that have similar habits being affected simultaneously. For example, heather-feeding species were locally scarce in 1919 after 90 per cent parasitism of the larvae in the preceding year (Burras, 1931). In certain years, as in 1883, 1887 and 1893, relative scarcities of Lepidoptera as a whole were attributed by some writers to unusual abundance of parasites.

Records of low percentages of parasitism at times of host abundance may indicate that increases in the abundance of Lepidoptera were caused by decreases in attacks by parasites. For example, there was an extraordinary local increase of *Plusia interrogationis* L., in 1934 and 1935, and in the latter year no larvae of hundreds collected was parasitized, whereas normally about half the larvae are attacked (Gane, 1936); *Aglais urticae* L., was abundant in 1942 and no parasites were obtained from 500 larvae collected (Frohawk, 1942); *Pieris* spp. were abundant in 1939 and 1940, and collections of larvae revealed no parasitized specimens (Blair, 1939; Tulloch, 1939); and no parasitism was noted in a spectacular outbreak of *Euphydryas aurinia* Rott., in 1928 (Riley, 1928).

Some long-term changes in the sizes of populations have been attributed to parasites. For example, a colony of *Euphydryas aurinia* Rott., under observation for 50 years decreased steadily from its year of greatest abundance, 1896, to 1912, and the most important cause of the decline was said to be a species of braconid that was fairly common in 1894, was more common in 1895, parasitized about 75 per cent of the larvae in 1896, and from then to the end of the colony's career parasitized a higher percentage—sometimes 90 or 95 per cent (Ford and Ford, 1930); and *Nymphalis polychloros* L., was fairly common in Sussex up to 1910, but in 1911 all larvae collected were parasitized and the species was not seen there in the next 20 years (Bentall, 1932).

Though, as shown above, species that have similar habits may be unusually heavily parasitized at the same time, the incidence of parasitism in such species is not necessarily related. For example, broods of larvae of *Aglais urticae* L., may be heavily parasitized, whereas larvae of *Nymphalis io* L., on the same patch of nettles may be free from attack (Allan, 1943); and in 20 years, apparently because of parasitism, *Eupithecia albipunctata* Haw., became scarcer than *E. trisignaria* H.-S., which it formerly outnumbered by about ten to one, and disappeared from some of its localities, though the larvae of the two species are of the same size and occur on the same species of plant at the same time (Hayward, 1933).

The situation of host larvae may affect the incidence of parasitism. For example, some species of parasites may have an alternation of generations in different hosts, and their incidence of attack on species of Lepidoptera may depend to some degree on the availability of alternate hosts. In an outbreak of *Yponomeuta padella* L., on blackthorn growing on shingle, with no other blackthorn or hawthorn nearby, parasitism was by one species and was under one per cent, whereas a few miles away, where blackthorn and hawthorn were growing together under normal conditions parasitism was by seven species and was well over 45 per cent (Thorpe, 1944). It was stated that the more important of the parasites appeared to depend for the completion of their life-cycles on the presence of various other lepidopterous larvae —species that were almost certainly absent in the first locality.

There are indications that at least some species whose larvae feed within fruit or seeds are not heavily parasitized. Natural control probably is primarily by destruction of the larvae when the seeds or fruit are eaten by herbivorous or frugivorous animals. For example, the incidence of parasitism is negligible in *Lampronia rubriella* Bjerk., whose larva feeds within fruit of loganberry (Beirne, 1943; Hill, 1950), and in *Glyphipteryx cramerella* F., whose larva feeds within seeds of cocksfoot grass (Chopra, 1925).

Temporary changes in the life-cycle of the host or changes in the identity of the chief parasite can have detrimental effects. According to Collier (1953), destruction of larvae of *Limenitis camilla* L., by a braconid parasite became progressively greater after the summer of 1947, when the butterfly developed a partial second brood. In 1952 the species was not found in some localities where it was common in 1951, and in other localities its numbers had declined. This was attributed to a second species of braconid parasite that was first seen in 1952 and that replaced the first as the primary parasite.

c. Diseases.

Diseases caused by fungi, bacteria, viruses and protozoa are important in the natural control of British Lepidoptera, but their incidence varies so rapidly and extensively that it is impossible to indicate their importance as compared with that of other kinds of natural

enemies. Moreover, there are relatively few data on their effects in the field. Some reasons for this are that the incidence of disease in rearing cages does not necessarily bear any relation to its incidence under natural conditions, that deaths of larvae in the field often pass unnoticed, or at least unrecorded, and that the identification of the causative or organism of a disease is usually difficult or impossible in the field.

The published records indicate that the incidence and spread of disease is strongly influenced by weather conditions, a matter discussed later, and that the incidence of disease often depends on the abundance of the host. Some examples illustrate the importance of disease under normal conditions of host abundance: hibernating larvae of *Hydrillula palustris* Hübn., are said to be very subject to attack by a fungus (Edelsten *et al.*, 1944); hibernating larvae of *Enarmonia nigricana* F., are attacked by three species of fungi (Cameron, 1938); and in a field study of *Nymphalis io* L., at that time an uncommon species in the area investigated, the number of larvae decreased rapidly with each visit, and on each occasion numerous shrivelled larvae were found on the ground and the food-plant (Adams, 1945). However, there does not seem to be any evidence at present that disease is normally the chief controlling factor for any one species.

Records of the suppression of outbreaks by disease indicate that, if weather conditions are suitable, disease can cause more destruction more rapidly than other kinds of natural enemies. Polyhedral viruses commonly cause destruction of larvae of *Diurnia fagella* Schiff., *Orgyia antiqua* L., *Erannis progemmaria* Hübn., and *E. defoliaria* Clerck (Harrison, 1945). These are species whose females are flightless and in which, as explained earlier, there is a tendency for heavy populations to build up rapidly. Some examples illustrate the importance of disease in suppressing outbreaks: almost all the larvae in a severe outbreak of *Orgyia antiqua* L., died from disease, apparently bacterial (Massee, 1948); and in an outbreak of larvae of *Charaeas graminis* L., in 1937 the majority of the larvae that survived attacks by birds died from bacterial disease in the fourth and fifth instars, with the result that there was no infestation in 1938 (Cameron, 1938).

5. COMPETITION

Records of competition deal almost exclusively with the effects of competition for food. Competition for other resources of the environment, for instance, pupation sites, has apparently gone unrecorded.

Larvae may become so abundant in outbreaks as to eat all the available food and, as a result, die of starvation. This has occurred with *Tortrix viridana* L., *Hypocrita jacobaeae* L., *Euproctis phaeorrhoea* Don., *Nonagria typhae* Thunb., and the common 'Hyberniidae'. Other species on the same food-plant may be affected in the same way. There are records of scarcities of other oak-feeding species following defoliation of the oaks by larvae of *Tortrix viridana* L., and in some

instances the scarcities were said to have persisted for several years. Reductions in normal competition may have the opposite effects.

Local scarcities or extinctions of a number of local species, notably *Maculinea arion* L., have been attributed to grazing by sheep, cattle and rabbits, and in one instance to destruction of flowers of the food-plant by slugs. However, mortality by such animals is probably caused primarily by the early stages being trampled upon or eaten by the animals, rather than by actual competition for food. It is probable that birds and animals that feed on fruit, seeds or nuts may be important factors in the control of species whose larvae feed within them, but definite records of this were not available. However, there was said to have been destruction of larvae of *Eucymatoge pini* L., when the spruce cones within which they feed were eaten by squirrels (Nix, 1903).

6. RELATIONS WITH OTHER ANIMALS

Some insects that are not associated with Lepidoptera as predators or parasites or as effective competitors for food can affect the relative abundance. The extensive fluctuations in the abundance of wasps may affect the abundance of *Aphomia sociella* L., whose larvae inhabit the nests, and fluctuations in ant abundance may affect the abundance of *Maculinea arion* L., *Myrmecozela ochraceella* Tengs., and other species that are associated with ants in the early stages. Fluctuations in the abundance of hymenopterous galls on plants may affect the abundance of such species as *Pammene splendidulana* Guen., *P. inquilana* Flet., and *P. amygdalana* Dup., whose larvae feed in oak galls; and *Orthosia miniosa* Schiff., whose larvae eat galls in the two last instars, is said to be most frequent in a good 'gall year' (anon., 1951).

There is a body of opinion, indicated by published records (e.g., Rogers, 1909; anon., 1919), that the excretion of aphids known as honeydew is harmful to larvae. This was discussed by Allan (1945). Years of aphid abundance were bad or average years for Lepidoptera as a whole, but in each instance this could be attributed primarily to the effects of other controlling factors (Beirne, 1947). Years of aphid abundance had no apparent effects on the relative abundance of Lepidoptera in the year succeeding each; these latter ranged from bad to good in respect of the relative abundance of Lepidoptera as a whole. Scarcities of some Lepidoptera, notably noctuids, at times of aphid abundance may be apparent rather than real: moths are scarce at flowers and artificial baits because of the counter-attraction provided by the honeydew. In general, published records indicate that honeydew on the food-plants can be detrimental to larvae, but on a basis of existing information it is not possible to assess its relative importance as a natural control factor. The "cuckoo-spit" produced by froghoppers (Homoptera) also is said to cause deaths of larvae (anon., 1919).

7. FLUCTUATIONS IN ABUNDANCE OF NATURAL ENEMIES

Just as there are fluctuations in the abundance of Lepidoptera as a whole to which fluctuations in the abundance of individual species are not necessarily related, there are fluctuations in particular kinds of natural enemies, taken as a whole, to which fluctuations in the abundance of individual species are not necessarily related.

Birds were stated to have been unusually common in 1883 and 1893, but were relatively scarce in 1878, 1881, 1890, 1895, 1917, 1929, 1940, 1945 and 1947, and in some instances in the years immediately following each of these. Parasitic Hymenoptera, or parasitized lepidopterous larvae, were said to have been unusually common in 1883, 1887 and 1893, and locally in the spring of 1881 and in 1889, 1890, 1896, 1899, 1909, 1910 and 1948. They are said to have been scarce in 1882. Disease was apparently especially prevalent in 1887, 1888 and 1903. Mites on adult Lepidoptera were stated to have been more abundant than normally in 1889, 1902, 1903 and 1913. Wasps were exceptionally abundant in 1864, 1880, 1883, 1887, 1890, 1893, 1902, 1911, 1919, 1921 and 1935, and unusually scarce in 1865, 1879, 1886, 1894, 1897, 1903, 1910, 1918, 1920 and 1924. Odonata were said to have been relatively abundant in 1897, but scarce in 1903, 1908 and 1918. Ants were locally abundant in 1887, but scarce in 1921.

Among insects that are not natural enemies, but that may affect the abundance, aphids were especially common in 1889, 1893, 1898 and 1911, and probably also in 1907, 1929 and 1944, and hymenopterous galls were said to have been abundant in 1929, 1937 and 1938, but scarce in 1879.

8. RELATIONS WITH THE VEGETATION

Seasonal scarcities of species of Lepidoptera may occur when the life-cycles fail to coincide with the development of the food-plant or when there is a temporary scarcity of the food-plant, or of those parts of it on which larvae feed. Conversely, an abundance of suitable food may result in an increase; examples of this have been mentioned earlier.

Occasional differences in the relative rates of development of species of Lepidoptera and of their food-plants probably are usually caused by the weather. In the cold, wet autumn of 1891 many larvae were not full-fed before the trees lost their leaves (Adkin, 1892); and it has been stated that this commonly occurs with species such as *Calocasia coryli* L., and *Bena prasinana* L. (Holland, 1893). It has been suggested that seasonal scarcities of *Lithostege griseata* Schiff., may be the result of the species producing an abnormal second brood in the

previous autumn, and these larvae fail to reach maturity before the food-plant dies (Edelsten, 1914).

Differences in food-plant development may be caused by differences in the situations of individual plants. Trees unaffected by larvae of the 'Hyberniidae' were those that leafed late as compared with infested trees (Waterhouse, 1896); with *Tortrix viridana* L. similar differences in infestation are stated to be associated with the relation between time of egg-laying and the precise stage of bud development (Salisbury, 1944); peas sown early are much less liable to infestation by *Encarmonia nigricana* F., than those sown late (Smith, 1931).

Differences in food-plant species may affect the rate of development. Larvae of *Parascotia fuliginaria* L., that feed on fungus on birch are said to become full-fed more rapidly and to reach a larger size than larvae that feed on fungus on pine (Bretherton, 1946); and larvae of *Lasiocampa quercus* L., on bilberry feed rapidly, pupate in late May and early June, and, under favourable conditions, produce moths in August, whereas larvae on heather in the same localities hibernate at a smaller size, do not commence feeding until later, and as a result are half-grown when the bilberry-feeding larvae are spinning their cocoons (Fearnehough, 1946).

The composition of the vegetation and the relative abundance of the different species of plants in a community are important in regulating the relative abundance and the distributions of species of Lepidoptera. This is because the abundance and distributions of most species are determined primarily by those of the food-plants. Species that are restricted to one or a few species of food-plants are more strongly affected than those whose food-plant requirements are less limited.

The presence of plants other than the food-plants may be necessary for the occurrence of a species in a locality. These affect Lepidoptera primarily by determining the characteristics of the ecoclimate, but they also affect some species in other ways. *Argyroploce rufana* Scop., *Depressaria badiella* Hübn., and *Dolicharthra punctalis* Schiff., are usually found among plants such as gorse and bramble, though these are not the larval food-plants; *Sarrothripus revayana* Scop., *Zelleria hepariella* Stt., and *Acrolepia granitella* Tr., occur chiefly where trees such as yew and juniper provide the thick cover in which they hibernate, though their larvae do not feed on these trees; and *Conistra vaccinii* L., is said to be found mainly in the mature parts of woods where the previous year's bracken forms a thick undergrowth in which it hibernates (Collins, 1890).

The composition of the vegetation may also affect the abundance by affecting the activities or the local distributions of some natural enemies, for instance, by determining the number of suitable nesting-sites or the visibility of the prey to predators. Moorhens apparently

find pupae of *Nonagria cannae* Ochs., in stems of bulrush by sight, and pupae in stems growing among long grass are seldom attacked, whereas those in exposed stems nearby are attacked heavily (Wightman, 1935); the chief hymenopterous parasite of *Rhyacia buoliana* Schiff., feeds on flowers of Umbelliferae during the first part of its adult life, and the presence of these flowers may be an important factor in regulating its occurrence (Thorpe, 1944); and attacks on larvae of *Pieris rapae* L., by its chief hymenopterous parasite are more than twice as heavy on larvae on cabbages grown close together in sheltered gardens than on larvae in cabbage fields (Richards, 1940).

It is apparent that vegetational changes can, and do, result in changes in the distribution and abundance of Lepidoptera. These latter, unlike most changes caused by natural enemies or weather, are persistent or permanent rather than temporary. The majority of recorded distributional changes and persistent changes in the abundance have resulted from vegetational changes—most of them from vegetational changes that either were caused by man or arose from the ecological successions of vegetation that human activities permitted to commence. Such changes have been extensive (Beirne, 1947). Over periods of thousands of years major distributional changes caused by vegetational changes that were caused by climatic changes have taken place.

9. EFFECTS OF WEATHER

On a basis of the primary ways in which they affect Lepidoptera, weather factors may be classified broadly as (a) normal weather and (b) abnormal weather. The latter affect Lepidoptera in ways that are additional to those of normal weather, and because of this can cause marked and sometimes rapid changes in abundance.

Weather affects the abundance in various ways. The importance of the results of its effects on the activities of the adults should not be underestimated. The species are at their lowest abundance in the adult stage of the life-cycle. Consequently effective control factors at this time can be relatively important. The adults fly only when weather conditions permit, and the vagaries of British weather and the frequency of days or nights when few or no Lepidoptera are to be seen in flight show that conditions are unsuitable as often, or more often, as not. According to Stokoe and Stovin (1948), if the female is not mated within two or three days of its emergence from the pupa (except with hibernators) it appears to lose its attractiveness to the males. It is apparent that weather conditions that deter the males from flight, that disperse assembling scents rapidly, or that prevent females from egg-laying, could result in a marked reduction in the size of the next generation of a population. Conditions that favour these activities could have the opposite effect. Weather also affects the abundance and the activities of the natural enemies and the relative rates of development of Lepidoptera both directly and by destruction of the food-plants.

a. Normal Weather

(i) *Sunshine and solar radiation.* Sunshine as such is the chief factor that regulates the activities of the adults of most butterflies and other day-flying species. This affects the abundance. That of *Lycaena phlaeas* L., for example, appears to be directly related to the annual amount of sunshine (Beirne, 1947). In general, relatively sunny summers have been 'butterfly years,' e.g., 1892, 1911, 1921, 1933 and 1942, whereas butterflies were scarce in relatively sunless summers, e.g., 1886, 1894, 1902, 1920, 1924, 1931, 1937, 1948 and 1951.

The theoretical effects of fluctuations in solar radiation on insect abundance were discussed by Laidlaw (1951), who concluded that there is an optimum radiation for each species, which increases in abundance following this optimum. Species most affected by solar radiation, according to Laidlaw, are those whose larvae feed exposed to light, whereas those whose larvae prefer shade are less affected and those whose larvae feed entirely concealed are little affected. Fluctuations in solar radiation are associated with fluctuations in sunspot numbers. The latter fluctuate in cycles, of which the most clearly defined average 11.13 years in duration. Analyses of published data on fluctuations of individual species of native British Lepidoptera did not reveal fluctuations that could be correlated with the sunspot cycle, though MacLagan (1940) found association between outbreaks of *Charaeas graminis* L., *Plutella maculipennis* Curt., and cutworms with sunspot maxima. The effects of solar rediation on the abundance of Lepidoptera need investigation. British weather is so variable that any basic cycles of abundance or scarcity that may exist can be altered so frequently and easily by weather conditions of short duration that they are not apparent from existing descriptive records. However, it may not be coincidence that between 1864 and 1952 good years for Lepidoptera as a whole exceeded bad years in number during periods of sunspot increase and maximum, and bad years exceeded good years during periods of sunspot decrease and minimum.

On the subject of cycles, it may or may not be significant that the two long periods of successive bad and average years for Lepidoptera, which ended in 1886 and 1930, were 44 years apart; that, according to Russell (1952), periods when butterflies in the New Forest were exceptionally abundant, and unusually variable, 1896-7, 1918-9 and 1941, were 22 years apart; and that Barnes (1932) showed that the rainfall has decreased and increased in successive periods of about 22 years each.

(ii) *Moonlight.* Though moonlit nights tend to be bad for moths, this is primarily because the temperature and humidity of such nights tend to be relatively low (Williams, 1940). Such nights are often good if temperature and humidity are high. However, Williams (1936) showed that the phases of the moon have a marked effect on the activities of noctuids: an average of 2.7 times as many individuals

were captured in light traps at times of no moon as at times of full moon. This could affect the breeding and egg-laying, as, because of the effects of other weather conditions, the period when a species is in the adult stage frequently differs from year to year and may coincide with different phases of the moon in different years. However, definite examples of this cannot be given.

(iii) *Atmospheric pressure*. Atmospheric pressure has important effects on the activities of nocturnal moths. Williams (1940) found that high catches in light traps occurred with high atmospheric pressures, rising or steady, and with medium pressures, steady or falling; and low catches occurred with low pressures, rising, falling or steady, medium pressures rising, or high pressures falling.

(iv) *Wind*. Because of the brevity of the daily flight periods of most species and the broadness of available wind data, comparisons between the latter and the relative abundance of Lepidoptera are not feasible at present. However, there are many descriptive records that indicate wind, even of low velocity, is a deterrent to the activities of adult Lepidoptera. This, by influencing the breeding and egg-laying activities, can affect the abundance of the next generation of a population. Wind is apparently never beneficial to the activities of adult Lepidoptera, though its detrimental results on the abundance may be partly offset by the fact that it seems to be detrimental to the activities of parasitic Hymenoptera and other natural enemies. The latter is indicated by the greater activity of such organisms under windless conditions.

Evidence of the detrimental effects of wind is provided by many descriptive records of reductions in the numbers of Lepidoptera on the wing with the appearance or increase of wind. Supporting evidence is provided by the greater abundance of Lepidoptera in sheltered as compared with exposed situations. The more weakly-flying species are the more seriously affected. For example, in a very windy locality butterflies and noctuids were numerous, geometers were poor in numbers, and tortrices were very scarce (Longstaff, 1902). Some species are less affected than others by normal winds: *Notodonta anceps* Goeze and *Hydrillula palustris* Hübn., are said to fly on wild nights; and wind before the end of May has relatively little effect on the activities of the early spring species (Haggett, 1947).

It is difficult to see how air movement as such, other than high winds which are discussed later, deters Lepidoptera from flight. It seems probable that the chill factor, rather than the actual air movement, produces the effects: to an animal, moving air feels colder than still air of the same temperature. There is a considerable difference between the chill factor of windless conditions and that of conditions of slight wind (5 m.p.h. or less). The chill factor increases more slowly with higher wind velocities. It is significant that Williams (1940) found that a wind of two m.p.h.—a barely perceptible breeze—reduced light-trap captures by half as compared with conditions

of no wind, and that higher wind velocities caused further reductions, but at lower rates. It is a matter of common observation that the activities of butterflies and other sun-loving species are less affected by moderate winds than are those of crepuscular and nocturnal species. This is probably because the temperature in the sunshine is much higher than in its absence, so that the chill factor is much lower.

Cold east or north-east winds in spring are especially detrimental to Lepidoptera in Britain, and there are many records of their disastrous effects on the numbers of Lepidoptera on the wing. The detrimental effects may be because the chill factors of such winds are relatively high, because of their dryness: according to Manley (1952), over the temperature range 35 to 50 deg. F. dry air is more cooling than moist air, which explains the cutting qualities of a dry north-east wind in spring, even though the temperature may approach 50 deg. F. Such cold winds have been recorded as killing larvae, both directly and by killing the food-plants.

(v) *Temperature*. Published evidence and opinions leave little room for doubt that warm weather in spring, summer and autumn is favourable to the abundance of most species of Lepidoptera, and that cold weather is unfavourable. Since 1864 about half the summers that were colder than the average were bad for Lepidoptera, whereas almost half those that were warmer than the average were good. Temperature produces its results on the abundance by affecting the activities and the rates of development of all stages of Lepidoptera, the activities of the natural enemies, and the rates of development of the food-plants.

Williams (1940) concluded that temperature is probably the most important factor in regulating the activities of nocturnal moths: the best nights for captures in light traps were about 9 degrees Fahrenheit warmer than the poorest nights, and the catch was doubled by an increase of 5 degrees in the minimum temperature and by one of 7 degrees in the maximum. According to Williams (1952), a very large portion of the mean changes in populations in the field can be accounted for by the effect of rainfall and minimum temperature in the three previous months. According to Evans (1948) a drop in temperature, especially in early spring, induces many moths to remain in the one spot without moving: a specimen of *Pheosia gnoma* F., remained nine days without movement. This is important in view of Stokoe and Stovin's (1948) statement, already quoted, on the loss of attractiveness of females to males.

Reductions in breeding and egg-laying activities that follow reductions in activities caused by unfavourable temperatures can result in scarcities or extinctions. In north-east England in the cold, wet summers of 1902 and 1903 *Aglais urticae* L., which swarmed in 1901, was nearly extirpated, *Maniola jurtina* L., and *Coenonympha pamphilus* L., became extinct over wide areas, *Erebia aethiops* Esp., was not seen, and *Euchloe cardamines* L., became progressively scarcer in the

following years (Harrison, 1939); 1921 was a bad year for some species, despite the warm summer, and it was suggested (Morley, 1922) that species that had been partly exterminated by the cold summer of 1920 had not re-established themselves in their normal numbers; and the Dorset population of *Papilio machaon* L., disappeared in 1816, a year that had the lowest accumulated summer temperature for 60 years (Bretherton, 1951).

High temperatures often increase rates of development. In long, warm summers, as in 1893, 1896, 1905, 1911, 1933 and 1945, there were abnormal supplementary broods of many species. These could influence the relative abundance in the following summers, as the larvae may die if they do not reach maturity before the food-plant dies or loses its leaves in the autumn. Examples of this were given earlier. In cold summers, as in 1888, some normally double-brooded species may be single-brooded.

Effects of temperature at times when the species are in active stages of the life-cycle must vary greatly, depending on the frequency and force of the wind. Some warm years seem to have been less good than others for Lepidoptera. In some instances this may have been partly because the favourable effects of the temperature were reduced by winds. Similarly, winds may cause temperatures that are themselves not unfavourable to become unfavourable, which may explain why some years in which conditions of temperature and rainfall were not unfavourable were bad for Lepidoptera. Possibly the chill factor may be the cause of some of the many changes in the relative abundance of individual species that cannot be associated at present with environmental changes.

Judged from published records, there has been a widespread belief that mild winters are unfavourable to the abundance of Lepidoptera as a whole. However, comparisons between the average winter temperatures and the relative abundance of Lepidoptera in the following summers did not support this. The comparison indicated a greater tendency for winters with about average temperatures to be followed by good years for Lepidoptera than winters that were distinctly warmer or colder than the average. Bad years that have been attributed to mild winters have had other causes. For example, a number of writers attributed the scarcity of Lepidoptera in 1882 to the preceding very mild winter, but, as will be shown later, high winds were the real, or at least the primary, cause. The view that mild winters are detrimental may have developed as a converse of the fact that some cold winters—those in which there were periods of severe cold —were very beneficial to the abundance of Lepidoptera. Winters that were colder than the average, but that did not include periods of severe cold, were not noticeably beneficial to the abundance.

The records indicate that the effects of winter temperatures vary with the species and depend to a large extent on their habits. According to Barrett (1882), noctuids whose larvae hibernate underground

and tortrices whose larvae hibernate within stems or roots are not affected detrimentally by mild winters, and similar views have been expressed by other observers. Barrett listed a considerable number of species that were very scarce in one region during a period when the winters were relatively mild, but that became common, and in some instances very abundant, after severe winters. Hibernating larvae do not appear to be affected detrimentally and were abundant in the springs of 1884, 1895 and 1948, following mild winters.

Though mild winters are not as harmful as has been sometimes supposed, there is no real evidence that they are beneficial to the majority of the species. The exceptions are a small number of maritime species that survive in the British Isles only in coastal regions where winter temperatures are high; these have been discussed elsewhere (Beirne, 1947).

Mild winters may be detrimental to those species that hibernate in unprotected positions because the activities of predators and the development of fungal diseases may be favoured by the mild weather. The beneficial results of severe winter cold on the abundance support this view. An additional factor that may be important to some species is that in a mild winter some larvae may fail to hibernate properly and are unable to undergo for a second or third time the physiological processes necessary for successful hibernation if disturbed by mild weather. The converse applies in severe winters, as in 1917.

(vi) *Rainfall and moisture.* More than half the summers that were wetter than the average were bad for Lepidoptera, whereas good years for Lepidoptera outnumbered both bad and average years in summers that were drier than the average. Summer temperatures have supplemented the effects of moisture. Summers that have been both colder and wetter than the average always have been bad or average for Lepidoptera, except when preceded by severe winter cold, and they have been followed by bad or average seasons, except when these were preceded by severe winter cold. Summers that have been both drier and warmer than the average have been good or average for Lepidoptera, except when there were droughts or other unfavourable weather extremes, and usually were followed by good or average years for Lepidoptera. Winters that were drier than the average were slightly more favourable, in respect of the relative abundance of Lepidoptera in the following summers, than winters that had about average rainfalls, and were considerably more favourable than wet winters. The average winter temperatures do not appear to have altered these effects. The main conclusions are that wet summers and wet winters are unfavourable to Lepidoptera, and that dry summers are favourable.

Relatively high or low rainfall over longer periods has similar effects. In the British Isles, 1865 to 1886 and 1909 to 1930 were wet periods, and 1887 to 1908 was a dry period (Barnes, 1932). During the drier period about half the summers were at least partly

good for Lepidoptera, whereas during the wetter periods barely one-third of the summers were at least partly good. Moreover, the too long periods of successive bad or average years for Lepidoptera, 1872 to 1886 (except 1881 and 1885) and 1919 to 1931 (except possibly 1928 and 1930), coincided with the latter parts of the wetter periods. The scarcity of Lepidoptera as a whole in Ireland as compared with southern England, which has been remarked by those experienced in collecting in both regions, may be partly because of the relatively much higher rainfall in Ireland.

Published records indicate that moisture may be detrimental primarily by causing deaths of larvae and pupae. For example, wet is said to be fatal to pupae and young larvae (Hall, 1888); occasionally many dead larvae are to be found under the soaked food-plant (Walsh, 1940); and young larvae of *Pieris rapae* L., have been found half-drowned in the water in cabbage leaves after rain (Richards 1940). The last two examples are of drownings, but normally the deaths are probably caused primarily by disease. Infection by fungal diseases is favoured by high humidity, and the higher the humidity the more rapid their development. The summers mentioned previously in which disease is said to have been especially prevalent were relatively wet. The summers, also mentioned previously, in which mites on Lepidoptera were unusually frequent were also relatively wet. It has been stated (Hewett, 1895) that wet is particularly harmful to larvae of Noctuidae but is less harmful to larvae of Geometridae.

Rain at night, as such, does not appear to affect the activities of nocturnal species, but rain during the preceding day is associated with a low catch in light traps (Williams, 1940). The reduction in sunshine that is usually a concomitant of excess rainfall or humidity has detrimental effects on the activities of sun-loving species.

Occasional changes in normal habits may render individuals susceptible to destruction by rain. Larvae of *Stenoptilia pneumonanthes* Buett., occasionally enter open flowers of the food-plant, instead of the buds, and are liable to drowning when the flowers fill with rainwater (Brown, 1938); larvae of *Celastrina argiolus* L., on holly, the usual food-plant, were drowned by rain, but those on Portugese laurel survived unharmed (Burrows, 1909); and, according to Smith (1931), larvae of *Agrotis segetum* Schiff., and other cutworms may have originally lived on the surface of the ground, but were able to adopt a subterranean habit when the soil was loosened and broken up by cultivation; rainfall in late spring governs the occurrence of outbreaks, and the reasons that have been suggested for this is that the water-logged condition of the soil may force the larvae to the surface so that they are exposed to attacks by predators.

Some species are apparently unaffected by excess moisture. For instance, the heavy rains of the summer of 1931 did not affect the abundance of *Cilix glaucata* Scop., *Odontosia carmelita* Esp., *Biston betularia* L., and *Apatele psi* L., which were unusually common

(Harrison, 1931). Others require moisture; for example, hibernating larvae of *Macrothylacia rubi* L., require a plentiful supply of moisture and larvae of *Pterostoma palpina* L., and of other Notodontidae require frequent rain showers, as does the larva of *Philudoria potatoria* L. Other species are favoured by the effects of moisture on their food-plants. Lichen-feeding species, in particular, are affected in this way. For example, *Cryphia perla* Schiff., was abundant in the wet summer of 1903 and very scarce after the very dry summer of 1893, and *Lithosia quadra* L., was very abundant in the very wet summer of 1879. It was suggested that a relative abundance of grass-feeding species in 1903 was a result of the wet summer of 1902 (Kaye, 1903); and a local abundance of *Vaccinium*-feeding species in 1878 was because of the very wet summer of that year (Hodgkinson, 1880).

b. Abnormal Weather.

Abnormal weather conditions, e.g., weather extremes and out-of-season weather, affect Lepidoptera in ways that are additional to those in which normal weather conditions operate. They have been the cause of the greater number of year-to-year changes in the abundance.

(i) *Severe cold.* Severe cold in winter has been more beneficial to the abundance of Lepidoptera as a whole than any other single weather condition. There were periods of severe cold in the winters of 1878-9, 1880-1, 1889-90, 1894-5, 1916-7, 1928-9, 1939-40, 1944-5 and 1946-7. The results were as follows: 1878 was a very bad year for Lepidoptera, but was followed by a steady improvement to the good year of 1881; the bad year of 1889 was followed by an improvement to the basically very good year of 1893; the bad year of 1894 was followed by a relatively good year; the average year of 1916 was followed by two good years; the about average year of 1939 was followed by a good year; the bad year of 1944 was followed by a good year; and the average year of 1947 was followed by a good year. There was apparently no marked increase following the winter of 1928-9, perhaps because the cold spell came so late in the winter, which reduced its effects, and because any beneficial effects may have been largely offset by the effects of the wet summer of 1929 and of the preceding succession of wet years. The latter factor may have been responsible for the rather slow increase following the cold of 1878-9. It is recorded that there was heavy mortality of bird-life in each of these cold spells, and that many species of birds took years to recover. As birds are important predators of most species of Lepidoptera, it is reasonable to assume that their scarcity was the primary cause of the increases in the abundance of Lepidoptera. Supplementary causes were that the hard condition of the ground, or the snow cover, protects subterranean larvae and pupae from attacks by predators—a local abundance of *Hepialus lupulinus* L., in 1947 was attributed to this—and the cold prevents larvae from moving about.

Not every species is benefited by severe winter cold. Populations of species that just reach the northern limits of their ranges in the

British Isles have been affected detrimentally. A flourishing population of *Eilema caniola* Hübn., disappeared in the cold winter of 1878-9 (Kane, 1893). Reports on the effects of severe winters on hibernating larvae and adults are conflicting: there were scarcities following some severe winters, whereas other severe winters had no apparent detrimental effects; similarly, hibernating larvae were abundant after some mild winters, but not unusually common after others. Possibly the winter temperatures may have relatively little influence on hibernating larvae, whose relative abundance in the spring may be regulated primarily by other conditions.

Frosts in late spring or early summer, after the species have come out of hibernation, are wholly detrimental. There are many records of their effects on Lepidoptera as a whole and on individual species. The results of the severe frost of 17th May, 1935, were well documented. Lepidoptera were killed directly and died because of frost damage to the food-plants. All butterflies on the wing at the time of the frost were killed (Tulloch, 1936); because of frost damage to the pupae, relatively large numbers of the moths that appeared later in the summer were crippled (Seabrock, 1935); young larvae were killed directly (Harrison, 1936); and Fletcher (1948) stated that *Tortrix viridana* L., had not been seen in one locality since the 1935 frost. The effects of frost damage to the food-plants were described by Edelsten (1935): the foliage of oak, ash and beach was completely destroyed and, as a result of the hot sun next day, became hard and brittle; a week later numbers of larvae, chiefly of Tortricidae, were still alive, but showed signs of starvation; after two weeks the new shoots were being gnawed by those larvae that had survived; many general feeders left the oaks and fed on the foliage of hazel, alder and birch; and it is believed that a great many larvae perished. Apparently the only recorded beneficial effect of a spring frost was the suggestion that a local abundance of *Celastrina argiolus* L., may have been because the frost caused heavier mortality to the parasite than to the larvae (Harper, 1945).

Frosts before most species have gone into hibernation are relatively rare in the British Isles. They have similar effects to spring frosts. Allan (1943) suggested that every larva of *Notodonta ziczac* L., over a wide area was killed by an October frost, and a local scarcity of *Arctia caja* L., was attributed to the same cause (Newman, 1907).

(ii) *Rainstorms and windstorms*. Heavy rainstorms and high winds are detrimental. They damage adults and knock larvae off the food-plants. The larvae may be prevented by the rain or wind from regaining their lost places on the food-plants and are more exposed to attack by parasites and predators, and they and the adults may be injured by swaying twigs, drowned by rain, or battered to death by rain or wind.

The results of the succession of high winds and gales of the summer and autumn of 1881 and the spring of 1882 were well documented.

In 1882 there was a marked scarcity of species whose larvae feed on trees, but species that fed on or near the ground in the previous autumn were in their normal numbers, and species whose larvae live internally in plants or in rolled leaves apparently were unaffected and became abundant in 1883. A few species that feed on low plants were affected: the winds destroyed seed-capsules and flowers of *Silene* spp., causing local scarcities of *Hadena caesia* Schiff., and *H. lepida* Esp. Salt storms, such as occurred in 1882 and 1938, are particularly destructive to larvae and food-plants.

There are a number of descriptions of severe destruction of adults by rainstorms, and some local scarcities in the same or in the following years have been attributed to this. There are records of larvae being washed off the food-plants. Outbreaks of some species, for example, *Tortrix viridana* L., *Charaeas graminis* L., and *Plutella maculipennis* Curt., have been checked by heavy rains. It has been stated (Webb, 1895) that larvae are less badly affected by heavy rains in woods than in exposed positions, such as on the Downs. In general, heavy rainstorms seem to be an important cause of mortality.

(iii) *Floods and erosion.* The effects of floods and erosion, which may result from gales or other weather extremes, are restricted in area. Local scarcities of maritime species, such as *Hadena andalusica* Stwd., *Arenostola morrisii* Dale, and *Panaxia dominula* L., have been attributed to cliff falls; local scarcities of *Leucania pallens* subsp. *favicolor* Barr., and *Euchloris smaragdaria* F., have been attributed to the flooding of coastal marshes by the sea; great numbers of buried pupae were killed when the Horsey Mere area was flooded by the sea (Ellis, 1938); and some species were reduced in numbers by the great sea floods of 1952. Records of the results of freshwater floods are surprisingly few. In general, floods in winter or early spring seem to have little or no harmful results. Possibly their harmful effects on Lepidoptera may be offset by the harmful effects on the natural enemies. Larvae of *Nonagria cannae* Ochs., were drowned when the water rose over the exit-holes in the stems of bulrush (Bowles, 1895), and there was increased destruction of pupae of *Nonagria* spp. when a high water-level enabled moorhens to find them more easily (Harper, 1947). Local scarcities of *Plusia festucae* L., have resulted when streams overflowed their banks and washed away the larvae.

(iv) *Drought.* Though warm, dry, sunny weather is, on the whole, beneficial to most species of Lepidoptera, many species are affected unfavourably when drought conditions develop.

The most striking effects are on noctuids, whose larvae pupate in the soil. There are numerous records of scarcities of such species in dry summers, as in 1857, 1864, 1893, 1896, 1898, 1905, 1919 and 1949. Most writers attributed the scarcities to the hard condition of the ground preventing the adults from emerging from the pupae. It seems probable that many pupae may be killed directly by desiccation. In a very hot season only one pupa of every 20 or 30 collected

on sandhills was alive (Balding, 1885). Another cause of mortality that has been suggested (Tutt, 1895) is that larvae have to travel greater distances to find suitably soft soil in which to pupate, and are consequently more vulnerable to attack by natural enemies. There are indications that larvae may be killed directly by drought. Larvae were abundant in the spring of the great drought year of 1893, and species whose larvae were full-fed before the drought were not scarce in 1894, whereas those whose larval period coincided with the drought failed to appear in many instances in 1894. Desiccation of the food-plants may cause mortality of larvae. *Lycaena phlaeas* L., was absent from many of its localities in the long, hot summer of 1921, though it is a species that normally increases in abundance with increased sunshine. Finally, hot, dry, sunny weather is favourable to the activities of important natural enemies, notably birds and parasitic and predatory insects. Some writers attributed the increasing scarcity of Lepidoptera in 1893 to the fact that natural enemies were exceptionally common in that year. 'Wasp years' are also years in which April, May and June are exceptionally dry. A feature of the abundance of Lepidoptera as a whole is that drought years almost always have been followed by years in which the abundance, judged from the descriptive records, decreased as the season progressed. Either the following year started as good and became less good, as in 1888 and 1905, started as good and became average or bad, as in 1912, started as average and became bad, as in 1893, 1896, 1898, 1922 and 1936, or started as bad and became worse, as in 1894 and 1919.

The increase in the abundance of some sun-loving species in drought years may mean that a greater number than usual may disperse from the breeding-grounds. Two of the most remarkable years on record in respect of the quality and quantity of immigrant Lepidoptera reaching the British Isles were 1945 and 1947, and in each of these there was said to be the most severe drought in more than a century in those regions of the Continent whence the migrants probably came.

10. MAIN FACTORS IN FLUCTUATIONS

It is apparent from the foregoing that most major fluctuations in the abundance of British Lepidoptera were caused primarily by fluctuations in the abundance of natural enemies that were mainly caused, either directly or indirectly, by weather changes. The second most important cause of fluctuations was the influence of weather on the activities of adult Lepidoptera.

The relative importance of weather factors that affect large areas simultaneously, and the relative importance of their detrimental as compared with their beneficial effects, is indicated by comparing changes in the abundance of the Lepidoptera as a whole from one year to the next, with the salient weather characteristics of the times the changes occurred. Most changes from bad to good years can be

associated without difficulty with weather extremes or other striking weather conditions. However, changes from good to bad years cannot always be associated with striking weather conditions. The probable reason for this is that natural enemies rather than weather conditions may have been primarily responsible for many changes from good to bad years. The build-up of populations of Lepidoptera in a good year must be followed by build-up of populations of their natural enemies, particularly of their parasites, which then reduce the Lepidoptera in abundance. Increases in the natural enemies are probably the main reasons why good years have occurred only singly or in twos, unlike bad or average years, which have occurred in longer successions.

Predisposing conditions for good or bad years for Lepidoptera as a whole are that factors that can cause major increases or decreases, respectively, in the abundance are not operating significantly. Given these conditions, the main factors in causing good years apparently were, in order of importance: (a) severe cold in the preceding winter, which apparently produces its effects mainly by killing or inactivating natural enemies; and (b) warm, dry weather (but not a drought) in summer, which favours the development of the early stages and the activities of the adults, and reduces the incidence of certain diseases. The main factors in causing bad years have been, in order of importance: (a) good years immediately preceding, in and following which populations of natural enemies built up; (b) relatively high rainfall over a number of successive years, which apparently produces its effects primarily by increasing the incidence of certain diseases; and (c) droughts and (d) late spring or early summer frosts, both of which kill Lepidoptera directly. Locally, and occasionally over wide areas, other detrimental factors that operate directly, notably rainstorms and windstorms, are important.

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SIPHONAPTERA FROM GLOUCESTERSHIRE, 2

By R. S. George, F.R.E.S.

The main purpose of this short note is to bring forward records of three fleas hitherto unknown from Gloucestershire so that they may be included in a survey of the recorded distribution of British fleas which is being compiled by my very good friend, Mr. F. G. A. M. Smit.

Family HYSTRICHOPSYLLIDAE

Subfamily RHADINOPSYLLINAE

Rectofrontia pentacantha (Rothschild) 1897, 2 ♂ 3 ♀ from nest material (probably *Clethrionomys*) found in a farm-yard, Brookethorpe, GE, 22nd November, 1953, *S. F. Lodge.*

Family LEPTOPSYLLIDAE

Peromyscopsylla silvatica spectabilis (Rothschild) 1898, 1 ♀ from nest material, Maisemore, GW, 8th July, 1954, *R. S. George.*

Family CERATOPHYLLIDAE

Subfamily CERATOPHYLLINAE

Malaraeus penicilliger mustelae (Dale) 1878, 5 ♂ 4 ♀ from the same material as *pentacantha;* 1 ♀ from nest material (believed *Microtus*), Uley, GW, 25th September, 1954, *M. Collins & A. Iles;* 2 ♀ from ♀ *Clethrionomys glareolus,* Podsmead, GE, 25th September, 1954, *R. S. George.*

With further collecting I hope that at least the following eleven species will as yet be found within this area:—

Typhloceras poppei Wagner 1903 (on long-tailed field mice),
Rectofrontia isacantha (Rothschild) 1907 (on the bank vole),
Palaeopsylla kohauti Dampf 1911 (on the mole),
P. soricis soricis (Dale) 1878 (from shrews),
Ischnopsyllus elongatus (Curtis) 1832 (on the noctule bat),
I. intermedius (Rothschild) 1898 (on the noctule and serotine bats),
Nycteridopsylla eusarca Dampf 1908 (also from the noctule),
N. longiceps Rothschild 1908 (on the pipistrelle and long-eared bats),
Ceratophyllus vagabundus insularis Rothschild 1906 (from jackdaws' nests),
C. garei Rochschild 1902 (in various birds' nests from low-lying and damp positions),
C. rossittensis rossittensis Dampf 1913 (in crows' nests).

Five small errors in my previous list (*antea*:— **5**: 85-94) should be corrected:—
p. 88, 1. 8, for *Archaoepsylla* read *Archaeopsylla.*
p. 88, 1. 12 up, for *Parsus* read *Parus.*
p. 89, 1. 17, for *brittanicus* read *britannicus.*
p. 89, 1. 9 up, for *octatenus* read *octactenus.*
p. 93, 1. 7 up, for November read October.

1 Podsmead Place, Gloucester.
4th October, 1954.

THE OLD DAYS AT CHATTENDEN ROUGHS

By H. C. Huggins, F.R.E.S.

Chattenden Roughs, a big wood about one mile from Cliffe station in Kent, first became famous in the early seventies. By that time Birch Wood and Darenth (locally prounounced Darn) were over-collected and becoming worked out, so collectors began to go farther afield. Chattenden at that date harboured many attractive insects amongst which may be mentioned *Aporia crataegi* I., *Melitaea athalia* Rott., *Aptura iris* L., *Agapetes galathea* L., *Nola albula* Hübn., *Siona lineata* Scop. and *Euenaemidophorus rhododactyla* Schiff. Of these *crataegi* and *athalia* soon disappeared, although not as far as I can ascertain from over collection. I still keep as a curiosity a somewhat crippled *crataegi* given me by the gamekeeper at Chattenden in 1901, but taken some twenty-five years before, which he told me was the last taken in the wood. The great attractions, however, were *iris* and *albula*, the latter, then called the Kentish Arches, was for many years supposed to be confined to Chattenden in this country.

My acquaintance with Chattenden began in 1900 and my information as to the palmy days before 1890 is derived from A. B. Farn and my father's factotum Blake. Farn needs no introduction, but a few words about Blake may be interesting as he represented a type extinct in the welfare state, and one on the whole that is best out of the way.

Many Victorian and Edwardian households had a kind of cadger and odd-job man. with no particularly defined duties, of which Blake was a sample. He was expected to do rough digging in the garden, carry coal, chop wood, carry bags to the station, exercise the dogs, feed the fowls, drown she-cats and generally make himself useful to mankind and an ornament to society. Blake, however, was a man of some little intelligence and in a rough way a naturalist. He could skin animals and birds and set them up in a somewhat terrifying fashion (the ghastly grin of my aunt's late cat, Toby, was legendary in the family) and was a professional collector of butterflies. There were a number of these in the district at that time, of whom the chief were Doran, who caught Farn's famous black *galathea* at Lodge Hill, then a part of Chattenden, and Packman, a celebrated *iris* catcher.

Packman always wore a top-hat when collecting and pinned his *iris* in it. On one occasion when Farn met him at Chattenden he proudly showed him a very fine *iole* pinned in the crown. Farn at once offered him £5 for it, which he accepted on condition he might take it home and set it. Of course Farn demurred to this and found his reason was that unless he showed them the butterfly Packman thought none of his friends would believe him, so Farn gave him a letter describing the insect and naming the price paid and carried it off safely.

Apart from these two leaders, however, there were many lesser men, of whom Blake was one, mostly pretty rough characters. The

great place for the *iris* was a row of several tall oaks on the highest point of the wood, growing on the side of a wide ride and the method of capture the long-handled net, with a thirty foot pole. There was great rivalry between these men and Blake often told how when an *iris* appeared two would rush at it at once and pretending to have their eyes on the sky, run violently into each other and try and knock each other over.

These happy encounters frequently wound up in a fight which sometimes degenerated into a free-for-all.

At the same time that the black-guard element was exterminating *iris* on the top of the hill the 'gentlemen collectors' were doing their best to perform the same service for *albula* and *rhododactyla* in the open plantation at the bottom. One sportsman collected a whole sack of rose-buds for the larva of *rhododactyla,* taking every bud that showed a thread instead of examining it, and the take of *albula* can be gauged from the hundreds, nay thousands, that have come under the hammer in old collections, all removed from the eight-acre plantation to which it was confined.

It is scarcely to be wondered at that the then Earl of Darnley, the rather fiery Edward Bligh, who was himself, though a non-collector, an enthusiastic naturalist, decided to put an end to these performances and closed the wood to collectors.

It is also not remarkable that directly he had done so he received a furious letter from that self-appointed champion of the down-trodden, the late J. W. Tutt. The correspondence went on in a varying degree of acrimony for some time until at last Lord Darnley gave way and gave Tutt personal permission to go, whereon Tutt promptly wrote that he had no intention of going but had protested on principle. Tutt being thus disposed of the wood was closed for some years until on Lord Darnley's death his successor, the famous cricketer Ivo Bligh decided to give permits to the decently behaved. His keeper's task was made much easier however by the extermination of *iris* before the wood was closed and the severe reduction of *albula, lineata* and *rhododactyla,* which only survived in very small numbers.

I always had permission to collect on all the extensive Darnley lands, Cobham, Cuxton, Luddesdown, etc., but did not go regularly to Chattenden until 1901. There were still plenty of nice insects about. I never saw *albula* except three larvae the keeper took in 1902 for Lord Clifton, the present Lord Darnley, and *lineata* was very rare, I only saw half-a-dozen, the last in 1903. I do not think either insect was taken there after the dates mentioned. *Rhododactyla* was gone from its former haunts but the Rev. C. R. N. Burrows in 1902 discovered it on the outskirts of the wood and showed me how to find it and it was present in varying numbers (due to heavy parasitism) until I gave up going to Chattenden and is still found in the district.

The keeper, Peek, had a cottage near the plantation, and here most of us arrived about four o'clock to have tea, which his wife made for

us. He also kept a good stock of beer on hand and would 'treat' anyone who wanted it to a bottle and of course expect a substantial tip in return. I met many of the old generation of collectors there, Prout with his tawny beard, sing-song voice and green leno net, Tunaley, Porritt, Joseph Ovenden, Tutt's brother-in-law, and last but not least Colonel Partridge, complete with tweed Norfolk jacket, Panama hat and a brown silk Kite net as big as himself. Partridge, who then lived at Blackheath, used to sleeve caterpillars in the wood just outside the keeper's garden, where they would be safe. He used to fix a flowerpot supported by a wire cage in the bottom of a special sleeve for those requiring earth for pupation. I well remember also his 'having me on' in the train when he, Burrows and myself were in the same carriage, by challenging me to identify the larvae of *Diphtera alpium* Osbeck, with the confidence of twelve I of course pronounced it *salicis*.

Ovenden was a very clever collector, now forgotten. When Mr. Burrows and I first met him and his wife I introduced C.R.N.B. (I had seen Ovenden before). Ovenden turned to his wife and remarked 'So that's Mr. Burrows, Mrs. O., you've heard a lot about Mr. Burrows from Tutt' This rather annoyed dear old Burrows who said that Ovenden called his wife 'Mrs. Ho', and he never referred to him afterwards by any title other than 'Mr. Ho'. Ovenden was a good man, however, and knew the micros as well as he did the macros.

The end of Chattenden as a collecting ground came in the 1914 war, the plantation and open woodlands where the rarer insects had been found becoming hopelessly overgrown. When I visited the place in 1922 the plantation was a wood forty feet high and the only good insect surviving was the light local form of *Perconia strigillaria* Hübn., in a rough meadow nearby and Mr. Chalmers-Hunt informs me that this has long since been extinct. Sic transit gloria!

ADDITIONS TO THE LEPIDOPTERA OF PUTNEY

By H. D. SWAIN, F.R.E.S.

The following species of Lepidoptera have been recorded within the area of Putney as described in *Ent. Gaz.* Vol. **3**, No. 3, July, 1952, in addition to those already listed.

SPECIES	DATE AND OTHER NOTES
RHOPALOCERA	
HESPERIIDAE	
Hesperia malvae L.	Quite common on Wimbledon Common.
HETEROCERA	
NOTODONTIDAE	
Drymonia ruficornis Hufn.	2 at light, May 1954
Cerura furcula L.	1 at light. May 1953
Stauropus fagi L.	1 at light. July 1952
Notodonta ziczac L.	1 at light. June 1953
LASIOCAMPIDAE	
Malacosoma neustria L.	1 at light. June 1954
DREPANIDAE	
Drepana lacertinaria L.	1 at light. June 1953
ARCTIIDAE	
Eilema lurideola Zinck.	1 at light 3.6.1953
AGROTIDAE	
Apatele alni L.	1 at light. June 1954
Amathes triangulum Hufn.	2 at light. July 1953
„ *xanthographa* Fabr.	Common; accidentally omitted from previous list.
Hadena suasa Schiff.	1 at light. June 1953
„ *contigua* Vill.	1 at light. June 1953
Cerapteryx graminis L.	1 on Wimbledon Common 21.8.1953
Zenobia subtusa Fabr.	1 at light July 1954
Dicycla oo L.	1 at light. July 1953
Orthosia advena Schiff.	1 at light. May 1954
Cucullia chamomillae Schiff.	1 at light. May 1954
PLUSIIDAE	
Rivula sericealis Scop.	2 at light. July 1952 and August 1953
Laspeyria flexula Schiff.	1 at light. July 1953

SPECIES	DATE AND OTHER NOTES
GEOMETRIDAE	
Perizoma flavofasciata Thunb.	Fairly common
" *bifaciata* Haw.	2 at light. June 1952
Hydrelia flammeolaria Hufn.	1 at light. June 1952
Lyncometra ocellata L.	2 in garden. June 1953
Xanthorhöe ferrugata Clerk	4 specimens. 3, June 1953, 1, June 1954
" *spadicearia* Schiff.	1 specimen. June 1954
Dysstroma citrata L.	1 at light. 1953
Mysticoptera sexalata Retz.	2 specimens. June 1953
Anaitis efformata Guen.	1 specimen. May 1953
Nycterosea obstipata Fabr.	2 specimens. June 1952
Eupithecia abbreviata Steph.	1 at light. May 1954
" *denotata jasioneata* Crewe	1 at light. June 1953
" *haworthiata* Doubleday	1 at light. July 1952
" *castigata* Hübn.	1 at light. June 1952
" *satyrata* Hübn.	1 at light. June 1952
" *tripunctaria* H-S.	1 at light. June 1953
" *nanata* Hübn.	1 at light. Sept. 1954
Bapta temerata Schiff.	1 specimen. June 1953
Campaea margaritata L.	1 specimen. June 1953
Ellopia fasciaria L.	1 specimen. June 1953
Ectropis extersaria Hübn. (*luridata* Borkh.)	1 specimen. June 1954
PYRALIDAE	
Aphomia sociella L.	Fairly frequent
Crambus pinellus L.	1 specimen. August 1953
" *margaritellus* L.	1 specimen. August 1953
" *pratellus* L.	Common
" *pascuellus* L.	Common
" *contaminellus* Hübn.	Sometimes fairly common
" *geniculeus* Haw.	Very common
" *inquinatellus* Schiff.	Common
" *tristellus* Fabr.	Not common
" *culmellus* L.	Very common
Chilo phragmitellus Hübn.	Rare, absent in some years
Schoenobius forficellus Thunb.	Rare
Acentropus niveus Ol.	Rare. 1952-53
Homoeosoma binaevella Hübn.	Common
" *sinuella* Fabr.	Common
Phycita betulae Goeze	Common
Acrobasis tumidana Schiff.	Rare
Dioryctria mutatella Fuchs	Fairly frequent
" *fusca* Haw.	Rare
" *splendidella* H-S.	1 specimen. July 1953
" *hostilis* Steph.	Rare
Euzophera suavella Zinck.	Rare
" *advenella* Zinck.	Fairly frequent
" *pinguis* Haw.	Common
Myelois cribrumella Hübn.	Fairly common
Hypochalcia ahenella Hübn.	Rare
Endotricha flammealis Schiff.	Very common
Aglossa pinguinalis L.	Rather rare
Pyralis glaucinalis L.	Fairly frequent
" *costalis* Fabr.	Very common

SPECIES	DATE AND OTHER NOTES
Synaphe angustalis Schiff.	1 specimen. June 1953
Scoparia ambigualis Treit.	Uncommon
„ *mercurea* Haw.	Common
Nymphula stratiotata L.	Rare
„ *nymphaeata* L.	Fairly common up to 1953 absent in 1954
Mesographe forficalis L.	Very common
Notarcha ruralis Scop.	Very common
Nomophila noctuella Schiff.	Common in the Autumns of 1951-53
Loxostege verticalis Hübn.	Common
Eurrhypara hortulata L.	Abundant
Hapalia ferrugalis Hübn.	Rare in 1951-52. Not seen in 1953 or 1954.
Anania verbascalis Schiff.	Rare
„ *nubilalis* Hübn.	Quite common
Pyrausta purpuralis L.	Rare
„ *aurata* Schiff.	Common
„ *coronata* Hufn.	Very common

PTEROPHORIDAE

Emmelina monodactyla L.	Common
Platyptilia calodactyla Hübn.	Not common (2 or 3 in 4 years)
Alucita pentadactyla L.	Fairly common

Several species, e.g. *Apatele alni* L., *Malacosoma neustria* L., *Drymonia ruficornis* Hufn., *Zenobia subtusa* Fabr., *Orthosia advena* Schiff., *Cucullia chamomillae* Schiff., *Xanthorhoë spadicearia* Schiff., and *Eupithecia nanata* Hübn., are new arrivals in 1954, but many others previously recorded have not put in an appearance during this very wet and cold summer.

A very dark specimen of *Hydriomena furcata* Thunb., was taken on 15th July, 1953. This example has the forewings nearly black with a quite black spot near the apex. The cross-lines are practically indistinguishable.

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